



## Diversity of liverworts and hornworts in *Polylepis sericea* forests in the Andes of Venezuela

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With 3 figures and 1 table

**Abstract:** The *Polylepis* forests of the high Andes host a unique biodiversity of plants and animals, yet are widely being destroyed by fire and cattle grazing and are considered as one of the most threatened ecosystems of South America. We inventoried liverwort and hornwort diversity in seven *Polylepis sericea* stands in the Andes of Venezuela (Sierra Nevada National Park) between 3400 and 4150 m. Hornworts were very few but liverworts were plentiful. Most of the species occurred on non-tree substrates (soil, rock, rotten wood), and less than one third were epiphytes. The relatively low number of epiphytic species and the prevalence of the smooth mat life form were indicative of relatively dry climatic conditions in the investigated forests. The strongly exfoliating bark of *P. sericea* may also have inhibited the epiphytic diversity. High species turnover between the two main study sites (Loma Redonda station, Sierra de Santo Domingo) probably reflected a 500 m elevational difference between the sites. Many species reached highest elevational occurrence in the forests and seven species were new to Venezuela (*Anthoceros tristianus*, *Kurzia brasiliensis*, *Lophocolea tenerrima*, *Metzgeria agnewiae*, *M. jamesonii*, *Plagiochila cleefii*, *Riccardia wallisii*). The new name *Frullania intumescens* var. *closterantha* (Spruce) Gradst. & Pócs comb. nov. is proposed. Almost half of the liverwort species had predominantly Andean ranges and seven species were largely restricted to the northern Andes. The elevated number of liverwort species with restricted ranges underscores the significance of *Polylepis* forests as a habitat for liverworts and their importance for conservation. The important role of saxicolous, lignicolous and terrestrial species in shaping liverwort and hornwort diversity in the Venezuelan *Polylepis* forests indicates that non-epiphytic taxa should not be neglected in studies on liverwort and hornwort diversity of these forests.

**Key words:** Anthocerotophyta; biodiversity; bryophytes; life form; Marchantiophyta; phytogeography; *Polylepis* forest; tropical Andes

## Introduction

Forests dominated by species of the genus *Polylepis* Ruiz & Pav. (Rosaceae) occur above 3000 m in the tropical Andes. They are considered the world's highest forests in terms of elevation and appear as arboreal islands in a matrix of grassland and scrub (Kessler 1995, 2006). These forests host a unique biodiversity of plants and animals and are an important supply of resources for local people, e.g., as firewood and building material (e.g., Fjeldså & Kessler 2004, Romoleroux et al. 2016). However, *Polylepis* forests are widely being destroyed by fire and cattle grazing, and are considered as one of the most threatened ecosystems of South America (Hensen et al. 2011, Caiza et al. 2019).

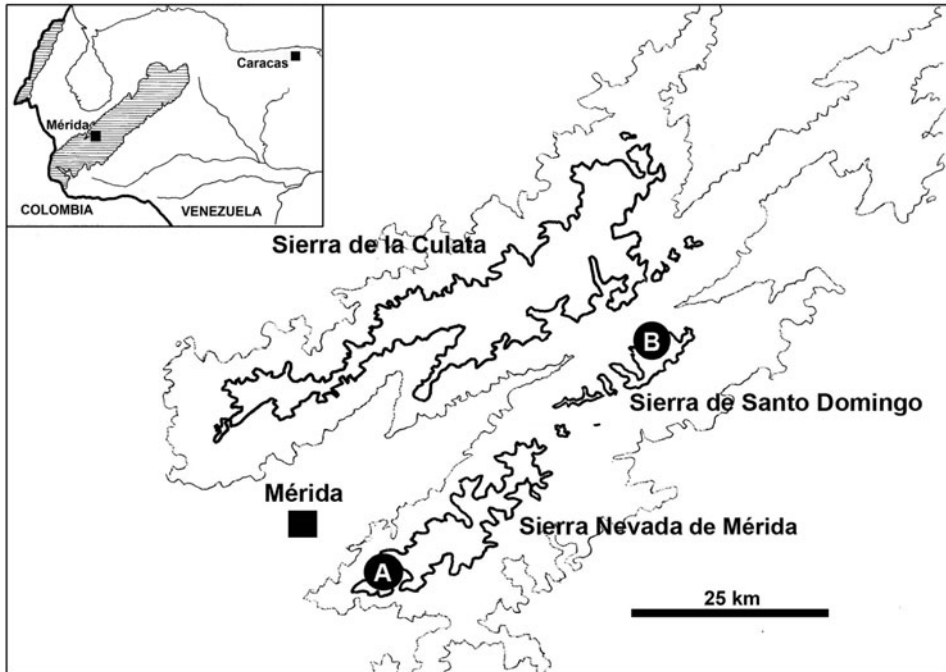
*Polylepis* contains about 30 species (K. Romoleroux pers. com.), with species diversity being highest in Bolivia and Peru and lowest in Venezuela where a single species occurs, *P. sericea* Weddell (Monasterio 1980, Kessler 1995). Characteristic of *Polylepis* trees are the gnarled shape and twisted trunks and branches, being considered adaptations to growth in harsh environments. The bark of the trees is typically reddish in color (hence the local name “coloradito” tree) and is strongly exfoliating. In spite of their shredded bark, *Polylepis* trees may host a rich epiphytic flora (Sylvester et al. 2014, Delgado & León-Vargas 2017, Gradstein & León-Yáñez 2017, 2020). Delgado & León-Vargas (2017) recorded 90 species of mosses in *P. sericea* forests of the Venezuelan Andes including a considerable number of epiphytic taxa (Delgado & León-Vargas 2017; precise number of epiphytic species not given). Seventy epiphytic liverwort species were recorded in *P. pauta* forests of Central Ecuador (Gradstein & León-Yáñez 2020). Diversity of mosses is highest in dry *Polylepis* forests while liverworts are most speciose in humid forests (Gradstein & León-Yáñez 2017, 2020).

The present paper focuses on liverwort and hornwort diversity in *Polylepis sericea* forests in the Andes of Venezuela. By comparing species richness, substrate preference, phytogeography and life form, we explore the importance of the Venezuelan *Polylepis* forests as a habitat for liverworts.

## Materials and Methods

### Study sites

Sierra Nevada National Park is the highest portion of the Venezuelan Andes, reaching to just over 5000 m on Pico Bolívar. The climate is relatively dry with a dry season of about 3–4 months and an annual rainfall of ca. 1550 mm (Monasterio 1980). *Polylepis* forests occur on steep rocky slopes up to about 4150 m in the Sierra Nevada de Mérida (Delgado & León-Vargas 2017). *Polylepis sericea* (“coloradito”) is the predominant tree species in these forests, being accompanied by species of *Gynoxys* Cass. and *Libanothamnus* Ernst. Common understory plants include species of the genera *Valeriana* L., *Senecio* L., *Gnaphalium* L., *Berberis* L., *Ribes* L., *Geranium* L., *Bartsia* L., *Oxalis* L., *Lachemilla* (Focke) Rydb. and various members of Ericaceae (Delgado & León-Vargas 2017).

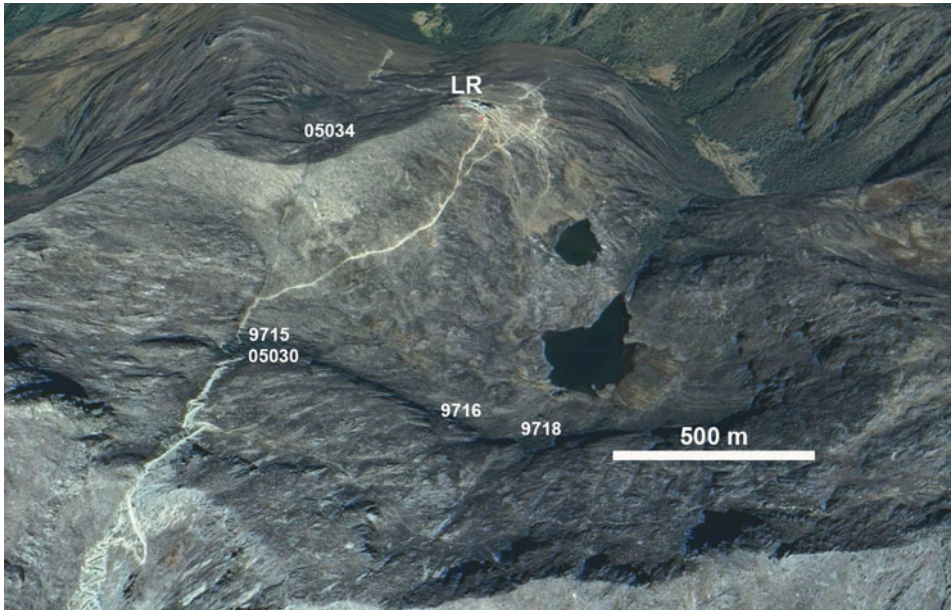


**Fig. 1.** Main locations of the investigated *Polylepis sericea* stands in the Andes of Venezuela (= hatched area, insert map). A: Sierra Nevada de Mérida. B: Sierra de Santo Domingo. Areas above 3000 m are marked by thin contour lines, above 4000 m by thick contour lines (modified after Delgado & León-Vargas 2017).

In February 1997 and April 2005, the second author had a chance to collect bryophytes in the *Polylepis* forests of Sierra Nevada National Park (Sierra Nevada de Mérida, Sierra de Santo Domingo; Fig. 1). Fieldwork in 1997 was made possible at the invitation of Dr. Yelitza León-Vargas of the Botanical Garden of the University of Mérida and in 2005 at the invitation of Ricardo Rico-Ramón of the same university. Seven *P. sericea* forest stands, each about one hectare in surface area, were inventoried, five near Loma Redonda station in the Sierra Nevada de Mérida (locs. 9715, 9716, 9718, 05030, 05034; Figs. 2–3) and two in the Sierra de Santo Domingo (locs. 9723, 05027; Fig. 3). All forest stands are located on outcrops or fissured rocky debris in páramo, above 3000 m. Some results of the floristic inventory carried out in 1997 were published by León-Vargas et al. (1998). The locations of the inventoried *Polylepis sericea* forest stands are as follows:

**A.** Sierra Nevada National Park, Sierra Nevada de Mérida, Teleférico de Mérida, surroundings of Loma Redonda station, 3900–4150 m, isolated *P. sericea* forests in páramo (Figs. 2–3):

**9715:** along trail to Los Nevados, below Alto de la Cruz, 8°32.5' N, 71°4.5' W, 4070–4100 m, 21–22 February 1997 (Fig. 3).



**Fig. 2.** Location of the five investigated *Polylepis sericea* stands in the Sierra Nevada de Mérida, near Loma Redonda station (LR) (modified from Google Earth).

**9716:** SSW of Laguna Los Anteojos, below NE facing cliffs,  $8^{\circ}32.10'$  N,  $71^{\circ}4.6'$  W, 4100 m, 21–22 February 1997.

**9718:** S of Laguna Los Anteojos, N side of a small valley,  $8^{\circ}32.1'$  N,  $71^{\circ}4.3'$  W, 3980 m, 21–22 February 1997 (= “Bosque 2”; Delgado & León-Vargas 2017) (Fig. 3).

**05030:** along trail to Los Nevados, below Alto de la Cruz,  $8^{\circ}32.2'$  N,  $71^{\circ}4.7'$  W, 4100–4150 m (6–8 April 2005) (= “Bosque 3”; Delgado & León-Vargas 2017) (Fig. 3).

**05034:** In the valley NW of Loma Redonda cablecar station, along Quebrada la Fría,  $8^{\circ}32.7'$  N,  $71^{\circ}4.8'$  W, 3940 m (8 April 2005) (= “Bosque 1”; Delgado & León-Vargas 2017) (Fig. 3).

**B.** Sierra Nevada National Park, Sierra de Santo Domingo, Páramo de Mucuchies, 3420–3600 m, *Polylepis sericea* forests in subpáramo around Laguna Negra:

**9723:** N of the laguna,  $8^{\circ}39'$  N,  $71^{\circ}49'$  W, 3420–3580 m, 2 March 1997.

**05027:** W of the laguna,  $8^{\circ}47'$  N,  $71^{\circ}48'$  W, 3450–3600 m, 5 April 2005 (Fig. 3).





**Fig. 3.** Images of investigated *Polylepis sericea* stands (photographs T. Pócs).

## Data collection and identification

In each forest stand liverworts were collected haphazardly on trunks, branches and twigs of *Polylepis* trees as well as on rotten wood, rock and soil. In total, about 115 collections were made, several of them containing more than one species. The collections were identified using mainly “The Liverworts and Hornworts of Colombia and Ecuador” (Gradstein 2020). For analysis of functional diversity of liverworts three broad functional groups were recognized following Gradstein & León-Yáñez (2020): 1) smooth mats (including tight mats and loose mats), 2) rough mats (including tails and wefts), 3) pendant species. Vouchers were deposited in herbaria MERC and EGR, with selected duplicates in GOET. The nomenclature of the species follows Söderström et al. (2016) and Gradstein (2020). Taxon authorities are cited in the species list.

## Results and discussion

### Species richness

The inventory yielded a total of 55 species, including 53 of liverworts and 2 of hornworts. The most speciose genus was *Metzgeria* Raddi (6 spp.), followed by *Frullania* Raddi, *Lophocolea* (Dumort.) Dumort. and *Plagiochila* (Dumort.) Dumort. (each 4 spp.). The two hornwort species were exclusively found in *Polylepis* forest in the subpáramo of the Sierra de Santo Domingo, reflecting the preference of hornworts for lower elevation habitats in the Andes, below 3000 m, and their scarcity in páramo. Indeed, only one hornwort – an undescribed species of the genus *Phaeomegaceros* R.J.Duff et al. – had hitherto been recorded from Venezuelan páramo (Sierra de Santo Domingo, 3600 m; Villarreal & Renzaglia 2006). The rest of Results and Discussion therefore focuses particularly on liverworts.

The largest number of species (44) was found in the *Polylepis* forests around Loma Redonda station while only 18 species were collected in the *Polylepis* forests of Sierra de Santo Domingo. Six species (ca. 10%) were shared by these two localities. The low number of species found in Sierra de Santo Domingo may be explained by the lesser forest stands inventoried there (2, vs. 5 in N.P. Sierra Nevada). The high species turnover among the two sites may reflect the elevational difference (500 m) between the sites and agrees with Delgado & León-Vargas (2017) who found high beta diversity in the moss flora of Venezuelan *Polylepis* forests.

### Floristics and phytogeography

Many liverwort and hornwort species reach highest elevational occurrence in the *Polylepis* forests of the Sierra Nevada de Merida and four species, *Acrobolbus cuneifolius*, *Frullania brasiliensis*, *F. montagnei* Gottsche and *Lophocolea tenerrima*, were found at much higher elevation than was previously known. Seven species are recorded for the

**Table 1.** Geographical ranges in the liverwort and hornwort flora of *Polylepis sericea* forests in the Andes of Venezuela.

Geographical ranges	Number of species
northern Andean (nA)	7 (12%)
tropical Andean (tA)	18 (33%)
Neotropical (N)	14 (26%)
Holarctic and extending into the Tropics (H)	3 (5%)
Wide-tropical and/or temperate (W)	13 (24%)

first time from Venezuela: *Anthoceros tristanianus*, *Kurzia brasiliensis*, *Lophocolea tenerrima*, *Metzgeria agnewiae*, *M. jamesonii*, *Plagiochila cleefii* and *Riccardia wallisii*. Five of them (*A. tristanianus*, *K. brasiliensis*, *M. agnewiae*, *P. cleefii*, *R. wallisii*) were already known from the Colombian Eastern Cordillera and their occurrence in the Venezuelan Andes was therefore to be expected.

A phytogeographical analysis of the liverwort and hornwort flora of the *Polylepis sericea* forests (Table 1) showed that about 45% of the species had predominantly Andean ranges; the remaining species (55%) had wider ranges and are Neotropical, wide-tropical or predominantly temperate taxa. The percentage of Andean species is slightly higher than in Ecuadorian *Polylepis* forests, which had 40% Andean species and 60% more wide-ranging species (Gradstein & León-Yáñez 2017). A much lower proportion of Andean species (18%) occurred in the moss flora of *P. sericea* forests of Venezuela (Delgado & León-Vargas 2017). Possibly this may be explained by a different definition of “Andean” species in the latter study. Most of the Andean species recorded in the present study are widely distributed throughout the tropical Andes and some of them extend to Mexico, southeastern Brazil and/or temperate southern South America. Seven Andean species are restricted largely to the northern Andes (*Acrobolbus cuneifolius*, *Lophocolea fragmentissima*, *L. tenerrima*, *Metzgeria jamesonii*, *Plagiochila cleefii*, *Ruizanthus venezuelanus*, *Syzygiella campanulata*), with some of them reaching northwards to Costa Rica. A similar number of rare, northern Andean taxa occur in *Polylepis pauta* forests of Ecuador, and two liverwort species, *Lejeunea mojandae* Gradst. and *Plagiochila pautaphila* Gradst. & León-Yáñez, are only found in these forests (Gradstein & León-Yáñez 2020). The elevated number of liverwort species with restricted, northern Andean ranges in *Polylepis* forests underscores the significance of these forests as a habitat for liverworts.

### Substrate preference and life forms

Seventeen species were growing as epiphytes on the *Polylepis sericea* trees (15 spp. at Loma Redonda, 2 at Santo Domingo); the remaining species (38) occurred on rotten wood, soil or rock. The epiphytic taxa included *Blepharolejeunea securifolia*, *Drepanolejeunea andina*, *Frullania montagnei*, *F. tetraptera*, *Lejeunea catimulifera*, *Leptoscyphus*

*physocalyx*, *Lophocolea bidentata*, *L. fragmentissima*, *L. muricata*, *Metzgeria* (6 spp.), *Microlejeunea capillaris* and *Plagiochila exigua*. Almost all of them (16 spp.) were smooth mats, one species was a rough mat (*F. montagnei*) and none of the species were growing pendant.

The number of epiphytic species found in this study – all of them liverworts – is rather low; 2–3 times more epiphytic species were recorded in *Polylepis pauta* forests of Ecuador (Gradstein & León-Yáñez 2020). The latter authors found highest species numbers in humid *Polylepis* forests while dry forests had rather few species. Furthermore, rough mats dominated in humid *Polylepis* forests while smooth mats prevailed in the dry forests. The low number of epiphytic liverwort species in the investigated *Polylepis* forests of Venezuela and the prevalence of the smooth mat life form concurs with the relatively dry climatic conditions in these forests, with a prolonged dry season. In addition, the strongly exfoliating bark of *P. sericea*, prohibiting the growth of epiphytes, may have played a role. Indeed, most of the liverwort species were collected on twigs and branches of the *Polylepis* trees, very few on the trunks which exhibited strongest shredding of bark. The impact of bark exfoliation of the *Polylepis* trees on the diversity of epiphytic bryophytes has not yet been studied in detail and needs investigation.

## Conclusions

1. *Polylepis sericea* forests are rich in liverworts but the majority of the species grow on non-tree substrates (soil, rock rotten wood). Less than one third of the species collected were epiphytes. The important role played by saxicolous, lignicolous and terrestrial taxa in shaping liverwort diversity in the Venezuelan *Polylepis* forests indicates that the non-epiphytic component should not be neglected in studies on liverwort diversity of *Polylepis* forests.
2. High species turnover between the two main study sites (Loma Redonda station, Sierra de Santo Domingo) may be due to the 500 m elevational difference between the two sites.
3. The relatively low number of epiphytic species and the prevalence of smooth mats are indicative of the dry climatic conditions in the investigated *Polylepis sericea* forests. The strongly exfoliating bark of *P. sericea* may also have inhibited the development of epiphytic liverwort diversity.
4. Many liverwort and hornwort species reach highest elevational occurrence in the *Polylepis* forests and seven species are new to Venezuela (*Anthoceros tristianus*, *Kurzia brasiliensis*, *Lophocolea tenerrima*, *Metzgeria agnewiae*, *M. jamesonii*, *Plagiochila cleefii*, *Riccardia wallisii*). The majority of the latter species were known from the Colombian Eastern Cordillera and their occurrence in the Venezuelan Andes was therefore to be expected.
5. Almost half of the species have predominantly Andean ranges and seven species are largely restricted to the northern Andes. The elevated number of liverwort species with



restricted ranges underscores the significance of *Polylepis* forests as a habitat for liverworts and the importance of their conservation.

## Annotated species list

Data on species distribution are based on Gradstein (2020) unless otherwise stated. For explanation of study sites see Materials and Methods. Abbreviations: A = Sierra Nevada de Mérida; B = Sierra de Santo Domingo H = Holarctic and extending into the Tropics; N = Neotropical; W = wide-tropical and/or temperate; nA = northern Andean; tA = tropical Andean. Species new to Venezuela are marked by an asterisk.

### 1. Hornworts

\* *Anthoceros tristanianus* Villarreal et al. – B (9723); rock; N.

*Anthoceros tristanianus* was originally described from the island of Tristan da Cunha and has recently been recorded from high elevations in Colombia and Mexico, above 2800 m (Vaña & Engel 2013, Peñaloza-Bojacá et al. 2020). **New to Venezuela.** Characteristic are the relatively large, brown spores, ca. 50–70 µm in diameter, with a distinct trilete mark, numerous sharp spines on the outer spore surface, and the inner spore surface with blunt papillae and with a larger wart (tubercle) in the centre of each of the facets bordered by the trilete mark. A large wart in the centre of each facet is also present in the Neotropical *A. tuberculatus*, but the latter species has smaller spores (less than 40 µm in diameter) and thalli with dorsal lamellae, and grows at much lower elevations (up to 1200 m in Colombia).

*Nothoceros* sp. – B (9723 ster.); rock.

### 2. Liverworts

*Acrobolbus cuneifolius* (Steph.) Briscoe (= *A. caducifolius* R.M.Schust.) – A (9716); rock; nA.

An uncommon northern-Andean species, originally described from Venezuela and found a few times in Colombia and Ecuador (Gradstein 2020). The species is recognized by leaves of sterile and male shoots with a narrow base and being sometimes caducous. The species usually occurs below 3000 m; the collection from Loma Redonda (4100 m) is the highest elevational record of the species.

*Anastrophyllum auritum* (Lehm.) Steph. – A (9715, 9718, 05027, 05030, 05034); rotten wood, rock, soil; W.

One of the most common species of the Neotropical páramos.

*Blepharolejeunea securifolia* (Steph.) R.M.Schust. – A (9715, 05034); bark; tA.

Widely distributed at elevations above 2500 m in the tropical Andes, reaching northwards to Mexico; also found on Mt. Itatiaia in SE Brazil (see map in van Slageren & Kruit 1985).

*Blepharostoma trichophyllum* (L.) Dumort. – A (9715, 9716, 9723, 05030); rotten wood, rock; H.

A widespread Holarctic species that extends southwards to the high mountains of East Africa and to the tropical Andes, where it occurs exclusively above 3000 m (see map in Gradstein & Vána 1987).

*Cephaloziella fragillima* (Spruce) Fulford (= *C. granatensis* [Spruce] Fulford) – A (9715); soil; N.

The most common *Cephaloziella* species in the Neotropics; also recorded from Madeira. *Cephaloziella granatensis* is a phenotype from high elevation with copious gemmae. The width of the leaf lobes, used by Fulford (1976) to separate *C. granatensis* from *C. fragillima*, overlaps.

*Drepanolejeunea andina* Herzog – A (9715, 9718, 05034); trunks, twigs; tA.

A northern-Andean species characteristic of páramo, up to 4400 m.

*Fossombronia peruviana* Gottsche & Hampe (= *Austrofossombronia peruviana* [Gottsche & Hampe] Crand.-Stotl. et al.) – B (9723); soil; tA.

A characteristic species of peaty soil along streamlets and mires in páramo and puna in the tropical Andes, sometimes growing submerged. For a detailed treatment of the populations from the Venezuelan Andes see Crandall-Stotler et al. (1999).

*Frullania brasiliensis* Raddi – A (05030); rock; N.

One of the most common Neotropical *Frullania* species, found from sea level to 3900 m. The collection from Loma Redonda (4100 m) seems to be the highest elevational record of the species.

*Frullania intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb. var. *closterantha* (Spruce) Gradst. & Pócs, **comb. nov.** (= *F. closterantha* Spruce var. *closterantha*, Trans. & Proc.

Bot. Soc. Edinburgh 15: 51 1884; *F. intumescens* var. *sabanetica* (Gottsche) Gradst.) – A (9718 c.per., 05034 ster.); rock; N.

A common Neotropical-montane species that contains two varieties, var. *intumescens* with a foliose appendage at the base of the stylus and var. *closterantha* (= var. *sabanetica*) without stylar appendage (Gradstein 2020). In the northern Andes var. *closterantha* seems to be the most common variety. Gradstein (2020) described the latter variety as var. *sabanetica* but the name var. *closterantha*, created as autonym with the description of *F. closterantha* var. *hylonoma* Spruce (1884), has priority (L. Söderström, pers. com.).

***Frullania montagnei*** Gottsche – B (9723); branches; N.

A rather widespread Neotropical species, occurring mostly below 2000 m. The collection from Sierra de Santo Domingo seems to be the highest elevational record of the species.

***Frullania tetraptera*** Nees & Mont. – A (9715); twigs; N.

A widespread Neotropical species, ranging from 1000 m to over 4000 m in páramo.

***Gongylanthus limbatus*** (Herzog) Grolle & Váňa – B (9723); soil; tA.

An uncommon tropical Andean species, reaching northwards to Panama and Costa Rica. The species resembles the common *G. liebmannianus* (Lindenb. & Gottsche) Steph. but differs in the apical leaf margin bordered by narrow-rectangular cells.

***Gymnomitrium truncatoapiculatum*** Herzog – A (9716); soil; tA.

A characteristic Neotropical-alpine species on soil in páramo and puna up to 4300 m.

***Herbertus acanthelium*** Spruce (= *H. juniperoideus* subsp. *acanthelium* [Spruce] K.Feldberg & Heinrichs) – A (05030); soil; tA.

A common species from high elevation (to 4300 m) in the tropical Andes, reaching northwards to Costa Rica and the Dominican Republic.

***Herbertus sendtneri*** (Nees) Lindb. (= *H. grossispinus* [Steph.] Fulford) – A (9715, 05034); rock, soil; W.

A very widespread and variable species, distributed at high elevation in the Tropics, central Europe and the Himalayas; in the Andes found up to 4350 m.

***Isotachis lopezii*** (R.M.Schust.) Gradst. – A (9715 c.sp.); soil; tA.

A characteristic terrestrial species of páramo, distributed in the tropical Andes and furthermore found in Costa Rica and Jamaica.

\* *Kurzia brasiliensis* (Steph.) Grolle – B (9723); rotten wood; N.

A rare South American species that was only known from Brazil and Colombia. **New to Venezuela.** The species is recognized by quadrifid, succubous leaves with a distinct lamina, being divided to the middle into four triangular lobes with a 3–4 cells wide base. In the other two *Kurzia* species, the leaves are transverse without distinct lamina, being divided to near the base into four subular lobes.

*Leiomitra flaccida* Spruce (= *Trichocolea flaccida* [Spruce] J.B.Jack & Steph.) – B (05027); soil; N.

A common Neotropical-montane species, found up to about 4000 m in the Andes.

*Leiomitra paraphyllina* Spruce (= *Trichocolea paraphyllina* [Spruce] Steph.) – B (9723); soil; N.

A robust species of montane cloud forest and páramo, recorded from the tropical Andes, Central America and the West Indies, to over 4000 m.

*Leiomitra tomentosa* (= *Trichocolea tomentosa* [Sw.] Gottsche) – A (9716); soil; N.

The most common and widespread Neotropical member of the genus *Leiomitra*, found in humid montane forests and páramo up to 4100 m.

*Lejeunea catinulifera* Spruce (= *Amphilejeunea viridissima* R.M.Schust.) – A (9718, 05030, 05034); bark, rock; tA.

A characteristic Neotropical-montane species occurring throughout the tropical Andes and also in the mountains of Central America, the Dominican Republic and on Mt. Itatiaia, SE Brazil (Bastos & Gradstein 2020).

*Lepidozia incurvata* Lindenb. – B (9723); rotten wood; tA.

A common Andean species that reaches northwards to Central America and southwards to Bolivia and southern Brazil.

*Leptoscyphus physocalyx* (Hampe & Gottsche) Gottsche – A (9718, 05034); bark, rock; tA.

A common tropical-Andean species, distributed from Venezuela to Bolivia in upper montane forest and páramo between 3100–4100 m. The oil bodies, which were unknown in *L. physocalyx*, are relatively large, 4–7 per cell, coarsely granular, of the *Calypogeia*-type. Coarsely granular oil bodies are unusual in *Leptoscyphus*, most species have finely granular, *Jungermannia*-type oil bodies (Gradstein et al. 2001).

***Leptoscyphus porphyrius*** (Nees) Grolle – A (05034); rock; N.

A common Neotropical species with a wide elevational range, from sea level to 4300 m.

***Leptoscyphus trapezoides*** (Mont.) L.Söderstr. (= *Lophocolea trapezoides* Mont.) – A (05034), B (9723); rock, soil; N.

A widespread Afro-American species, occurring in montane forests and páramo to over 4000 m. *Leptoscyphus trapezoides* was long placed in *Lophocolea*, but its characteristic yellow-brown color together with molecular evidence indicated that the species is a member of the genus *Leptoscyphus*.

***Lethocolea glossophylla*** (Spruce) Grolle – A (9715, 05030); soil; tA.

The only Neotropical member of a small southern-temperate genus, occurring at high elevation in upper montane forest and páramo from Bolivia to Mexico, SE Brazil and the Dominican Republic, to over 4000 m.

***Lophocolea bidentata*** (L.) Dumort. (= *Lophocolea coadunata* [Sw.] Nees) – A (9715, 9718, 05034); bark; W.

A very common and variable, heteroicous (autoicous or dioicous) species distributed in tropical and temperate regions of the world, from sea level to 4500 m in the Andes.

***Lophocolea fragmentissima*** R.M.Schust. (= *Campanocolea fragmentissima* [R.M.Schust.] R.M.Schust.) – A (9715, 9718, 05034); trunks, branches, twigs; nA.

A characteristic twig epiphyte of upper montane cloud forests and páramo in the northern Andes (3000–4100 m), ranging northwards to Costa Rica and the Dominican Republic.

***Lophocolea muricata*** (Lehm.) Nees – A (9718); bark; W.

A widespread species of southern-temperate regions and tropical montane forests, in tropical America ranging from ca. 1000–3900 m.

\* ***Lophocolea tenerrima*** Spruce – A (9715, 05027, 05030); soil; nA.

A rare species of high elevations in the Andes of Ecuador and in Costa Rica, occurring on shaded, moist soil between 2400–3700 m (Dauphin et al. 2018). **New to Venezuela.** The collections from Venezuelan *Polylepis sericea* forest constitute the highest elevational records of the species. Characteristic of *L. tenerrima* are the whitish-green plants with almost horizontally inserted leaves and strongly and irregularly fragmenting leaf lobes. In deep shade the plants may become very tiny and flagelliform, with the whole leaves being fragmented and reduced. The Venezuelan plants differ from those of Costa Rica and Ecuador in having slightly larger leaves (1–1.2 mm long; to 0.8 mm in plants from Costa Rica and Ecuador), longer uniseriate leaf tips (2–8 cells long; 1–3 cells long in plants

from Costa Rica and Ecuador) and slightly more numerous oil bodies (3–7 per leaf cell; 1–4 in plants from Costa Rica). Moreover, plants from locality 05030 (Pócs 05030/H) stand out by underleaves with a long tooth on the outer margins, ca.  $1/2 \times$  lobe length (tooth absent or very short in plants from Costa Rica and Ecuador). However, in the material from locality 9715 (Pócs et al. 9715/AR), the tooth on the outer underleaf margin was absent or very short, exactly like in the plants from Costa Rica and Ecuador.

***Lophonardia jamesonii*** (Mont.) L.Söderstr. & Váňa (= *Andrewsianthus jamesonii* [Mont.] Váňa) – A (05030); soil; W.

A characteristic species of páramo in the mountains of Central America and the tropical Andes, up to 4500 m; also in East Africa (see map in Gradstein et al. 1983).

***Marchantia plicata*** Nees & Mont. – B (9723); soil; tA.

A common Andean species, ranging from Venezuela to Bolivia, at elevations up to 4200 m.

***Marsupella miniata*** (Lindenb. & Gottsche) Grolle (= *M. andicola* R.M.Schust., nom. inval.) – A (05030); rock, soil; tA.

An uncommon Andean species from high elevation, up to ca. 4350 m, ranging from Mexico to northern Argentina.

\* ***Metzgeria agnewiae*** Kuwah. – A, B (05027, 05034); twigs; W.

A widespread ramicolous, Afro-American species, in the northern Andes occurring in montane forests and páramo up to about 4500 m (see map in Costa 2008 for the Neotropical range). **New to Venezuela.** The species is readily distinguished by the blue coloration of the thallus upon drying, the presence of attenuate branches, the 2(–3) cell wide surface of the midrib both dorsally and ventrally, the marginal thallus hairs 1–2 per cell, and the deeply concave gemmae, which are produced on the margins of the attenuate branches, near the branch tips.

***Metzgeria albinea*** Spruce – A (9718); bark, rock; W.

A widespread pantropical species, distributed in montane forests up to about 4000 m (see map in Costa 2008 for the Neotropical range). Two different phenotypes are seen in the Venezuelan *Polylepis sericea* forests: a pendant phenotype with revolute thallus margins and a prostrate phenotype with flat margins.

***Metzgeria consanguinea*** Schiffn. (= *M. temperata* Kuwah.) – A (9715, 9718, 05034); trunks, twigs; W.

A widespread pantropical species, ranging northwards to eastern North America and western Europe where the species was known as *M. temperata*; commonly growing as a



twig epiphyte in open environments, to about 4000 m in the northern Andes. Recorded new to Venezuela by León-Vargas et al. (1998). Plants from locality 9718 were very depauperate and produced thalli without costa.

\* *Metzgeria jamesonii* Kuwah. – A (9715, 9718, 05030, 05034); bark, rock, soil; nA.

A rare northern Andean species that was only known from the type from Ecuador (Pichincha, leg. W. Jameson, around 1850). **New to Venezuela**; surprisingly common in the *Polylepis sericea* forests of the Venezuelan Andes. The plants are characterized by the strongly blue-colored, convex thallus with plane or reflexed margins, a 2-cell wide dorsal and ventral surface of the midrib, and marginal hairs mostly one, sometimes two per cell. The gemmae, which were unknown in *M. jamesonii*, are discoid, ca 200 µm in diameter when mature, concave, with rhizoids, and blue-colored when dry, and originate from the thallus margins and on the ventral margins of the midrib, near the apex of the thallus, but not on the thallus surface. The Venezuelan plants differ from the type from Ecuador in having more convex thalli, marginal hairs frequently one per cell, and abundance of gemmae. Since the species is known from very few collections we hesitate to draw taxonomic conclusions from the observed morphological discrepancies. Further collections are necessary for clarifying the taxonomy of this interesting species.

*Metzgeria scyphigera* A.Evans – B (05027); twigs; W.

A widespread Afro-American species, that occurs in the Andes in humid montane forests and páramos up to 4200 m (see map in Costa 2008). Recorded new to Venezuela by León-Vargas et al. (1998).

*Metzgeria violacea* (Ach.) Dumort. (= *M. fruticulosa* [Dicks.] A.Evans) – A (9715); twigs; H.

Widespread in warm-temperate regions of the Northern Hemisphere, and extending southwards along the mountains of Central America and the Andean cordilleras to Tierra del Fuego. In tropical America occurring in montane forests and páramo to about 4000 m (see map in Costa 2008 for the Neotropical range).

*Microlejeunea capillaris* (Gottsche) Steph. (= *M. colombiana* Bischler) – A (9715, 05034); twigs; N.

A widespread Neotropical-montane species, in the tropical Andes occurring up to about 4800 m. Recorded new to Venezuela by León-Vargas et al. (1998, as *M. colombiana*).

*Noteroclada confluens* Taylor – B (9723); soil; tA.

Distributed throughout the mountains of Latin America from Mexico to Tierra del Fuego, occurring at about (1800–)2800–4300 m in the Andes and at lower elevation in SE Brazil and Tierra del Fuego (see map in Schuster 1983).

***Plagiochila bifaria*** (Sw.) Lindenb. – A (9716, 05030, 05034); rock; W.

One of the most common and variable Neotropical species in the genus, ranging from 500 m to about 4200 m and extending northwards to the Atlantic coast of western Europe (see map in Heinrichs et al. 2004). The plants from *Polylepis sericea* forest stand out by a weak, 1–2 cell wide leaf border of thicker-walled cells and occurrence on rock. In Ecuadorian *Polylepis* forests, *P. bifaria* usually grows on bark (Gradstein & León-Yáñez 2017, 2020). The taxonomic status of the Venezuelan plants deserves further study.

\* ***Plagiochila cleefii*** Inoue – A (05030, 05034), B (05027); rock, soil; nA.

An uncommon northern Andean species, known from Ecuador and Colombia, in páramo and *Polylepis* forests between 3150–4300 m. **New to Venezuela.** The oil bodies in *P. cleefii*, which were unknown, are homogeneous and rather small and numerous per cell, *Massula*-type. The leaves in the Venezuelan plants are sometimes rather short and broad, obovate to suborbicular (loc. 05030), resembling those of *P. vittiana* Inoue from Mexico. However, *P. vittiana* has very shortly decurrent dorsal leaf bases whereas in *P. cleefii* the dorsal leaf bases are longly decurrent.

***Plagiochila exigua*** (Taylor) Taylor (= *P. corniculata* auct.) – A (05034); bark; W.

A widespread species, occurring in the high mountains of tropical America and Africa, between 2000–4000 m, and extending into warm-temperate oceanic regions of the Northern Hemisphere where it grows at much lower elevation. Recorded from the Andes of Venezuela by Schuster (1980, as *P. corniculata*). The oil bodies in the Venezuelan plants differed from those observed elsewhere (Schuster 1980, Inoue 1987, Paton 1999) in being larger, completely filling the cell lumina. A further interesting observation was the pronounced difference in size of female and male plants, the latter ones being much more slender than female ones. The same observation was made in the Ecuadorian Andes, where *P. exigua* is very common in dry *P. pauta* forests (Gradstein & León-Yáñez 2020). The observed sexual dimorphism is apparently not uncommon in the genus *Plagiochila*, it is very characteristic of *P. bifaria* (Heinrichs et al. 1998) and has been recorded in several other *Plagiochila* species (Heinrichs 2002, Heinrichs et al. 2002), but not yet in *P. exigua*.

***Plagiochila fuscolutea*** Taylor – A (9716); rock; tA.

A common Andean species, occurring in upper montane forest and páramo up to over 4000 m, from Venezuela to Bolivia.

***Radula voluta*** Taylor – A (9718, 05034); rock; W.

A widespread amphi-atlantic species, occurring in W Europe and eastern U.S.A., tropical Africa and the Neotropics. In tropical America found in montane forests and páramo to over 4000 m.

***Riccardia hans-meyeri*** (Steph.) Meenks & C.De Jong (= *R. columbica* (Steph.) Gradst. & Hekking) – A (9716), B (9723); rotten wood, soil; tA.

A common species of upper montane forest areas and páramo in the northern Andes, ranging from Venezuela southwards to Central Peru, between 2700–4500 m. Recorded new to Venezuela by León-Vargas et al. (1998, as *R. columbica*).

***Riccardia poeppigiana*** (Lehm. & Lindenb.) Meenks & C.De Jong (= *R. cervicornis* [Spruce] Gradst. & Hekking) – A (9715), B (9723); rotten wood, roots; N.

Probably widespread in tropical America but distribution insufficiently known; in the Andes largely restricted to upper montane forest and páramo, above 2500 m.

\* ***Riccardia wallisii*** (Steph.) Gradst. (= *R. smaragdina* Meenks & C.De Jong) – A (05030, 05034); rotten wood; tA.

A robust tropical Andean species of upper montane forests and páramo, up to 4100 m. **New to Venezuela.** *Riccardia wallisii* is recognized by the irregularly winged thallus with a rather broad and flat axis and short and plump, obliquely spreading branches with decurrent bases and broad tips (Gradstein & Reeb 2019). The thallus margin cells are often thick-walled and the wings vary considerably in width. Plants with rudimentary wings have been called *R. smaragdina*.

***Ruizanthus venezuelanus*** R.M.Schust. – A (9715); soil; nA.

A rare páramo species known from the Venezuelan Andes, the Sierra Nevada de Santa Marta (Colombia) and Costa Rica, at elevations to about 4100 m.

***Schistochilopsis incisa*** (Schrad.) Konstant. (= *Lophozia incisa* (Schrad.) Dumort.) – A (9715, 9716, 05030), B (9723); soil, rock; H.

A widespread Holarctic species that occurs scattered at high elevation in Central America and in the tropical Andes, above 2500 m (see map in Gradstein & Váňa 1987). Recorded new to Venezuela by León-Vargas et al. (1998, as *Lophozia incisa*).

***Sphenolobus austroamericanus*** (Váňa) Váňa – A (9715, 9716); rock; tA.

A rare páramo species that has been recorded from Venezuela, Colombia and Bolivia, between 3750–4400 m.

***Syzygiella campanulata*** Herzog – A (05034); rock; nA.

An uncommon species of the upper montane and páramo belt of the Northern Andes, extending northwards to Costa Rica and the Dominican Republic. The collection from *Polylepis sericea* forest near Loma Redonda station is the highest elevational record of the species, which was known from 2700–3700 m in the Andes.

*Telaranea nematodes* (Austin) M.A.Howe – B (9723); rotten wood; W.

A widespread Afro-American species; in the Neotropics found in montane forests and páramo to over 4000 m (see maps in Gradstein et al. 1983, van Zanten & Gradstein 1987).

*Triandrophyllum subtrifidum* (Hook.f. & Taylor) Fulford & Hatcher – A (9715, 9716), B (05027); rock; W.

A widespread southern-temperate species extending northwards into the high mountains of tropical Asia (to the Philippines) and of tropical America (up to Mexico), where it occurs at elevations to 4500 m.

## Acknowledgements

We are grateful to Dr. Lars Söderström for calling our attention to the existence of the name *Frullania closterantha* var. *closterantha* and to an anonymous reviewer for constructive comments on the manuscript. The second author expresses his gratitude to Yelitza León-Vargas (Mérida, Venezuela) for inviting him and his wife to a training course and a collecting trip in the Venezuelan Andes in February 1997, and to Ricardo Rico-Ramón (Mérida, Venezuela) for organizing a collecting trip in the northern range of the Venezuelan Andes in April 2005 for the staff of the Botany Department of Eszterházy College, Eger. He furthermore thanks the Hungarian Academy of Sciences, CONICIT and FUNDACITE-Mérida for covering the travel and lodging costs.

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Manuscript received: August 12, 2020

Accepted: October 17, 2020

Responsible editor: J.A. Jiménez Fernández