
BRYOFLORA AND LANDSCAPES OF THE EASTERN ANDES OF CENTRAL PERU:

I. LIVERWORTS OF THE EL SIRA COMMUNAL RESERVE

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Abstract: A total of 171 liverwort species in 51 genera from 18 families have been identified to date from bryophyte collections made in the Cordillera El Sira, an isolated outlying range of the eastern Andes in central Peru. The El Sira uplift is steep, rugged and hyper-humid, with annual rainfall recorded in excess of 7500 mm. Collections were made across an elevational range of approximately 2000 meters on the eastern escarpment of the Cordillera. These reveal a diverse bryophyte assemblage with distinct distributional patterns reflecting climatic, edaphic and micro-habitat heterogeneity. 38 new distribution records for Peru are reported.

Abstracto: Un total de 171 especies de hepáticas en 51 géneros y 18 familias han sido identificadas, hasta la fecha, de colecciones de briofitas realizadas en la Cordillera El Sira, un área lejano y aislada de los Andes orientales en el centro del Perú. Las alturas de la cordillera El Sira son empinada, accidentada e hiperhúmeda, con precipitaciones anuales de más de 7500 mm. Colecciones se hicieron a través de un rango de altitud de aproximadamente 2000 metros en la vertiente oriental de la Cordillera. Estas colecciones revelan un conjunto diverso de briofitos con patrones de distribución distintos que reflejan heterogeneidad climática, edáfica y de micro-hábitat. Se reportan 38 nuevos registros de distribución para el Perú.

Keywords: Cordillera El Sira, Eastern Andes, liverworts, Neotropics, Peru

INTRODUCTION

The Cordillera El Sira is the easternmost outlying range of the Andes Mountains in central Peru. It has sufficient elevation to support Andean floral and faunal elements yet has no direct connection to the main chain of the Peruvian Andes (Cordillera Oriental), and is in fact circumscribed almost entirely by lowland Amazonian habitat

(Plate I, photo 3). Only in its extreme southwestern flank is it loosely linked to a series of adjacent Andean outlying ranges, collectively forming what is known as the Yanachaga-San Mathias-San Carlos-El Sira cordilleran complex, part of the UNESCO-designated Oxapampa-Ashaninka-Yanesha Biosphere Reserve. This region contains some of the last undisturbed ecosystems in the central rainforest region (selva central) of Peru, typified by wide elevational gradients and distinct forest types supporting a noteworthy biodiversity.

The tropical Andes are truly one of the world's great centers of biodiversity (Churchill *et al.* 1995). On the extremely steep and rainy eastern slopes of the tropical Andes, mosses and liverworts play a vital ecological role in regulating the hydrological cycle and conserving both soil and water (Pócs 1980). Despite their high regional diversity (Gradstein and Pócs 1989) and important role in ecosystem function, the bryophytes of Peru remain poorly known and under-represented among the bryoflora of tropical Andean nations. A detailed account of life forms and ecomorphological structures of epiphytic bryophyte communities found on the eastern slopes of the northern Peruvian Andes can be reviewed in Kürschner and Parolly (1998).



Figure 1. Location of study site (in black- see Fig. 2 for detail) and its position relative to the Yanachaga-San Carlos-San Matias-El Sira cordilleran complex.

In 2007 we initiated exploration of the isolated uplands of the El Sira Communal Reserve, focusing our efforts on its northern sector (see *Figure 1*). We chose this region in consideration of the fact that the highest peaks of the entire uplift are found here. Our point of

entry was along the Ucayali River (eastern) side of the cordillera. First clearing a trail system from the river to the base of the uplift, we established a base camp and conducted botanical exploration as we probed the steep eastern escarpment of the cordillera, seeking a manageable route to the upper elevation zones of the chain. Over several expeditions we established an elevational transect that passes through a diverse series of forests: from lowland Amazonian, climbing through premontane and transitional forest types, into pristine cloud forests and ultimately emerging into the unique elfin forest formations dominating the upper elevations in this section of the range (see *Figure 7*). Over the past decade we have continued to expand our trail system (see *Figure 2*), investigating a variety of abiotic factors in addition to making numerous botanical and zoological collections.

Our interdisciplinary exploration of the biota of the El Sira Communal Reserve has among its aims a deeper understanding of the unique elfin forest ecosystems of the eastern Andes, beginning with the approximately 20 Km² area of elfin forest habitats found along the upper elevations of our transect. A related goal is the identification of critical elements driving the process of landscape self-organization across our study site, which presents a diverse ecological mosaic arrayed across a remarkably steep topography-climbing more than 1500 meters elevation in under 6 Km of linear distance- embracing a wide variety of microhabitats. These aims require documentation of physical constraints – rainfall, elevation, temperature, topography, geomorphology, soil chemistry, wind and insolation – articulated both within and between- multi-species assemblages scattered across a unique environmental gradient.

We feel that patterns of diversity and distribution of bryophytes – a ubiquitous component of cloud and elfin forests along our elevational transect – provide a useful approach toward realizing these goals. Species-level distributional data afford the opportunity to evaluate the community-level role of bryophytes within and between habitats, and to explore their influence on multi-trophic landscape-scale processes. At minimum, these data provide a census of the bryoflora of a previously-unstudied region, and can form a basis for a wider evaluation of regional-scale bryophyte biogeography. In order to better place these collections within the context of local landscapes, a brief overview of the study area is presented.



Plate I. Photo 1. View of the highlands of the El Sira Communal Reserve from the Ucayali River, looking west. **Photo 2.** View of herbaceous-dominated elfin forest habitat (1A) atop the Ariapo plateau, looking west. Gallery forest (2A) habitat visible in lower elevations in the lower left of photo. **Photo 3.** View of elfin forest habitat (1A) from atop the Ariapo plateau, looking north. Ucayali River and highland ridges visible in the background. **Photo 4.** View of elfin forest habitat (1A) atop the Ariapo plateau, showing cliff faces of the northern escarpment of the plateau, looking west. **Photo 5.** View of semi-woody elfin forest habitat atop the Ariapo plateau, looking eastward. **Photo 6.** View of interior of elfin forest (1B) habitat atop the Ariapo plateau.



Plate II. Photo 7. View of elfin forest habitat (2B) along the steep slopes of the Ariapo uplift. **Photo 8.** View of open elfin forest formation on sand (2A) atop the Ariapo plateau. **Photo 9.** View of campsite in upper cloud forest (3A) habitat on the Ariapo uplift. **Photo 10.** View of interior of elfin forest (2B) habitat on steep slopes of the Ariapo uplift. **Photo 11.** View of stream bed in gallery forest (2A) habitat in steep-sided stream valleys atop the Ariapo plateau. **Photo 12.** View of lush bryophyte community at the base of waterfall in gallery forest (2A) habitat in steep-sided stream valleys atop the Ariapo plateau. **Photo 13.** View of the highest peaks of the Cordillera El Sira (ca. 2400 meters elevation) looking westward from herbaceous dominated elfin forest (1A) habitat atop the Ariapo plateau.

In lowland regions of eastern Peru, rivers often still serve as highways. Approaching our study area, travelling southward up the Ucayali River, at about 100 Km out from the city of Pucallpa, the uplift known locally as Cerro Ariapo comes into view (weather permitting). On a clear day it appears as a series of peaks rising steeply to the west of the river, but is actually the rim of a very large plateau emerging from behind a series of subordinate hills and ridges (*Plate I, photo 1*). The top of this “peak”, from the vantage-point of the river, is actually a near-continuous series of quartz-containing sandstone cliffs underlying a large undulating plateau on its northern (Iparia River) and eastern (Ariapo River) flanks. Elevations here reach slightly above 2100 meters (*Plate I, photos 2 and 3*), but the plateau descends gently to the west before climbing again to reach the highest peaks of the chain (*Plate II, photo 13*), at over 2400 meters elevation, approximately 15 Km distant.

Leaving the river, and passing through one of several native communities located in the buffer zone of the El Sira Communal Reserve, our trail approaches the eastern (windward) slopes of the cordillera El Sira, between the Iparia and Ariapo Rivers, both affluents of the greater Ucayali River watershed in Ucayali Department. At its upper elevations, atop the Ariapo plateau, our trail crosses over into Pasco Department, skirting the headwaters of the Chinchihuani stream, an affluent of the Rio Apurucayali, an affluent of the greater Pichis/Pachitea River watershed.

At the outset of our exploration, gradual, but recognizable, discontinuities in vegetation type were observed as we extended the transect. When exploring routes to ascend the uplift, climbing steep slopes and rocky cliffs, along ridgelines when we could, at various times we stumbled into new and distinctive patches of forest. Members of our team- local inhabitants of the villages of the buffer zone, at times visible far below on the Ucayali River floodplain- would reflect that we were entering a “new world” (*otro mundo*) on the mountainside. Not only vegetation, but animals and geologic features played a part in these reckonings. These natural landforms and distinct vegetation types informed our early characterization of what we referred to as “pisos” (floors) along our trails, and we could refer to them in numerical order, from bottom to top.

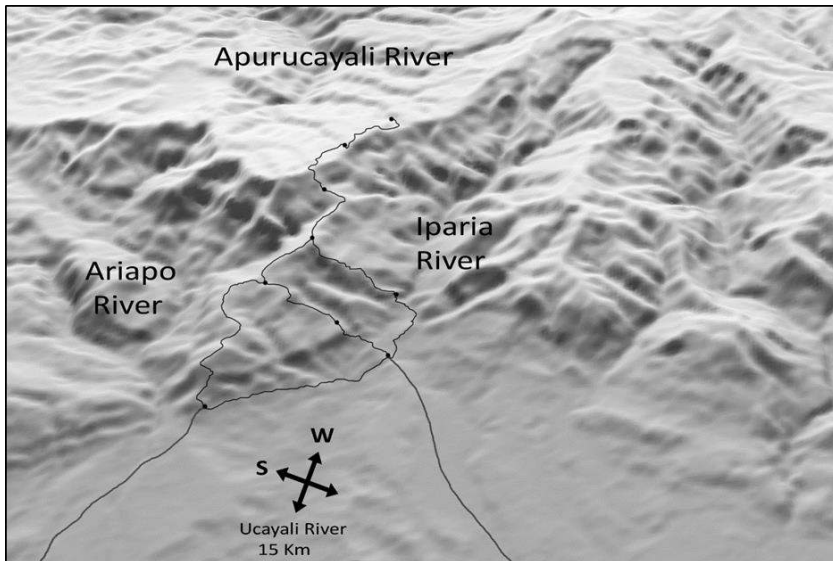


Figure 2. General landscape view of the study site, with trails and campsites illustrated.

MATERIALS AND METHODS

The liverwort collections presented here were made by J. G. Graham between 2007 and 2011 in the El Sira Communal Reserve, at elevations between 240 and 2100 meters. Both epiphyllous and other liverworts are represented. Sampling was limited mainly to the forest understory, up to about five meters in height (the maximum length of our pole pruners), and on fallen trees. Only in elfin forest formations could canopy sampling be routinely conducted. Collections were made at random, the main discriminating factors of our sampling being convenience (proximity to our trail and relative ease of access) and apparent diversity (perceptible difference from what had been previously sampled at a similar elevation). No statistically-validated sampling protocol was followed.

Specimens of non-epiphyllous bryophytes were shade-dried. Epiphyllous liverworts were collected along with their host-plant leaves, which were then pressed and dried in the field. All liverwort specimens were processed by M. Fischer (F) and identified by T. Pócs (EGR). A number of critical genera (like *Jungermannia*, *Plagiochila*, *Frullania*) await further investigation by specialists, and only a

smaller part of their species is represented here. Duplicate specimens of all collections are deposited at Herbario Forestal (MOL), Universidad Nacional Agraria Molina, Lima, Peru and Field Museum (F). Duplicate specimens of many of the liverworts reported here were deposited in the Herbarium of Eszterházy Károly University, Eger, Hungary (EGR). The description of environmental conditions including landscape analysis was made by J. G. Graham, while the taxonomic and phytogeographical evaluation of liverwort records were made by T. Pócs.

Temperature data were collected using Thermochron DS1922L iButton data logging devices, rainfall data were collected using Stratus RG202 Long Term Professional Rain Gauges. Representative soil data come from exposed mineral soil profiles in excavated soil pits. Soil samples were shade dried and characterized at the Soils Laboratory of the Universidad Nacional Agraria La Molina, Lima, Peru. Vascular plant data were provided from collections made by J. G. Graham.

RESULTS

Environmental gradients

Rainfall and temperature are probably the most important environmental factors in determination of vegetation zonation in tropical mountains (Frahm and Gradstein, 1991, Pócs 1977, 1994). Along our transect, altitudinal changes in environmental conditions occurring over a relatively short geographical range contribute to subtle transformations in forest structure and species composition. Environmental lapse rates along the transect have been measured to be around 5.3 °C/Km of altitude. These temperature changes affect evaporation, growth and decomposition rates, as well as a number of other biotic and abiotic functions.

Orography is the study of topographic relief of mountains, and orographic effects such as the interaction of the atmosphere with topography play a major role in defining the climate and habitat of our study area. The Cordillera El Sira, being the easternmost outlying range of the Andes in central Peru, as such receives some of the highest annual rainfalls recorded in the region. Prevailing easterly trade winds carry moisture from the Atlantic Ocean, along with abundant recycled moisture from the Amazon Basin. When this horizontally-flowing warm moist air mass encounters the cordillera,

it is forced upslope. As it ascends, this air expands and cools, allowing for condensation, cloud formation and precipitation.

Seasonal climate in the highlands of our study area can be broadly characterized as having a ten month wet season, from September through June (mean rainfall > 400 mm/month) and a 2-month dry season from July through August. Annual rainfall totals in our study area tend to be evenly distributed across all elevations. While there are slight differences between the four elevations at which we monitor rainfall (1800, 1500, 1000 and 400 meters), especially in the drier months, when it rains heavily it tends to rain heavily at all locations fairly equally up and down the elevational gradient. In contrast to our rainfall data collected over 5 years in the El Sira uplands, locations only a short distance to the east of the uplift (5-10 Km) show about a fourfold reduction in mean monthly and annual rainfall totals (see *Figure 3*).

Cloud formation and immersion most certainly play a major role in microclimatic variation (Romanski 2007), and the relative contribution of cloud-water to the hydrological cycle in the upper elevations in our study area is estimated to be a critical, but as-yet unquantified factor. We anticipate the installation of cloud-catchers to better monitor this phenomenon, but only anecdotal information is available at present. Fog frequencies are certainly greatest above 1000 meters elevation along the transect.

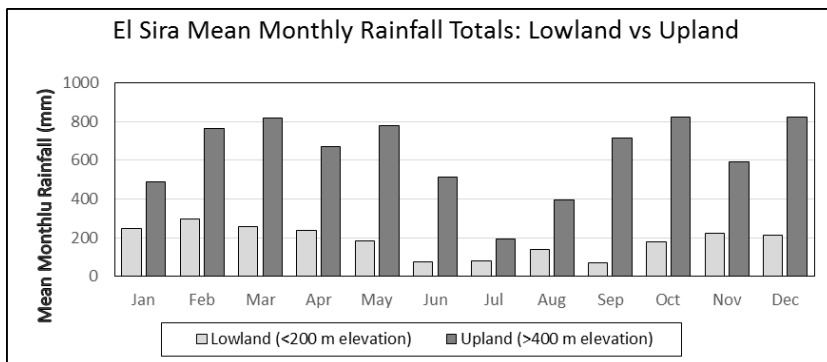


Figure 3. Mean monthly Rainfall (mm) comparing El Sira uplands vs. adjacent lowlands.

The relative precipitative contribution (where wind-driven fog particles are precipitated onto vegetation on contact) appears to be

a fairly localized phenomenon, dependent on temperature and humidity as well as exposure to prevailing winds, among other factors. It appears that the most important zone of cloud immersion along the transect is a narrow ridge at about 1500 meters elevation that divides the Iparia from the Ariapo River watersheds. Wind-driven clouds forming in the Iparia lowlands are commonly observed ascending the steep (northern-facing) slope of the ridge, skimming over the ridgetop and descending into the Ariapo basin. High epiphyte loads, bryophyte density and diversity are all found to occur here, despite the absence of a thick layer of poorly-decomposed organic material covering the soil (found at higher elevations) that serves as a readily-available surface for bryophyte colonization.

Mean annual temperatures along our elevational gradient vary at about one degree centigrade per 190 meters of elevation (between 400 and 2000 meters – see *Figure 4*). Once the transect reaches the top of the Ariapo plateau, which has relatively little altitudinal variation, temperatures are observed to vary only slightly, due primarily to habitat variation. Steep-sided canyons that cut across the plateau have lower mean temperatures, while mean temperatures measured on and below exposed cliff faces are slightly higher than what is predicted by elevation alone.

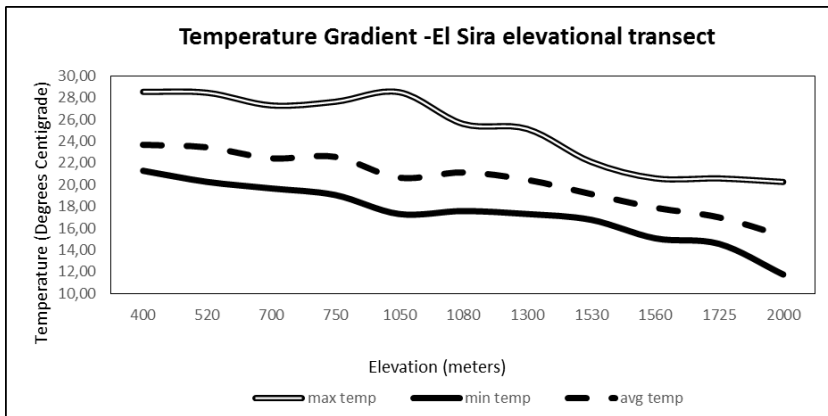


Figure 4. Temperature differentials measured along the slopes of our elevational transect in uplands of the El Sira Communal Reserve.

We initiated a series of soil plots along the transect, initially to try and identify factors that might explain divergent vegetation types

observed in the elfin forests found atop the Ariapo plateau. Plots were established along the transect, with measurement of woody vegetation surrounding each soil plot. To date we have established 27 soil plots. Of the 15 plots atop the plateau, 13 were on what was observed to be a heavy clay substrate of a variety of colors- brown to red to yellow to white- with three different vegetation types represented. Two plots were placed in narrow forested stream valleys transecting the plateau- these below sandstone cliffs contained coarse greyish sand soils. Five plots were located on the steep southeastern slopes of the uplift between 1900 and 1700 meters elevation. The upper two of these were of coarse greyish sand, the lower three were of mixed clay/sand. All of these (17) plots had a thick, spongy organic layer composed of mainly of fine roots of varying decomposition overlaying the mineral soil horizon.

Seven plots were established at elevations (from about 1600 meters) below where this organic layer disappears. One was established at about 1500 meters, consisting of what appeared to be dense, decomposed limestone, one was at about 1300 meters with heavy clay, one at 1100 meters with fine brown sand, two at 750 and 700 meters, both of dense yellowish clay, and one at about 500 meters, of fine reddish sand. One final soil plot was established in a unique low-elevation elfin forest formation at 1100 meters. This plot had a thick (25 cm) organic layer overlaying a mineral soil of dense reddish-brown clay.

From each soil-sampling site (one-meter-square at the surface- of varying depth) we sampled different soil horizons, measuring the thickness of leaf litter, of layers of undecomposed, moderately decomposed and finely decomposed organic material, as well as estimating the volume of rocks and/or large roots penetrating the organic layer and/or mineral soils.

Physical parameters noted in the field were elevation, slope, exposure, geographic coordinates and micro relief. In the plots with an organic layer overlaying the mineral soil horizon, we established a 100-meter-square area around the soil pit where woody vegetation was monitored, including number of stems, stem diameter at breast height (DBH), canopy height, and noting when horizontal trunks are present, as well as palms or tree ferns. In plots without an overlaying organic layer, we established 0.1 hectare plots, including number of stems, stem diameter at breast height (DBH) and individual tree height, including palms and tree ferns.

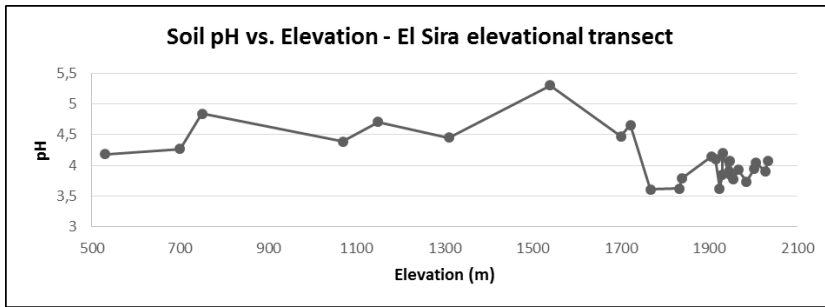


Figure 5. Soil pH as measured along our elevational transect in uplands of the El Sira Communal Reserve.

A number of soil physicochemical parameters, including pH, were characterized, and the assays revealed that the soils along the transect are remarkably acidic (see *Figure 5*). 74% of plots had soils characterized as extremely acidic (pH range 3.5–4.4), 22% were very strongly acidic (pH range 4.5–5), with 4% (a single plot) strongly acidic (pH 5.1–5.5).

Continuous abiotic data (temperature and elevation) corroborate much of our initial informal meso-scale recognition of landscape types, generally referred to by local indigenous assistants as *pisos*, or floors. The plot data- in particular the realization of two discontinuous soil types and the presence or absence of an organic layer capping the mineral soil present in the upper elevations of our transect - provided the data for further habitat sub classification.

Bryophytes are certainly not distributed uniformly across the elevational gradient of our study site. The addition of species-level floristic elements to our emergent habitat framework introduces another level of complexity, one that may allow further refinement of our concept of local landscape units. The following section will present our liverwort collections in this context, providing the raw data with which we can begin to explore relationships between these important biotic elements and their potential role in ecosystem organization.

Liverwort Collections

A total of 171 liverwort species are reported to date from our study site, from more than 600 collections, representing 16 families and 50 genera. These are presented in Table 1. It should be remembered that this list is only a fraction of the total bryophyte population at our study site, and that many important Neotropical liverwort families, as well as all the mosses, in our present collections are not represented here. Further botanical exploration is expected to expand the known distribution of liverwort species across the landscape, as well as introduce new species to our checklist. We look forward to further elucidation of patterns of bryophyte diversity and distribution, both across our transect as well as within the cis-Andean foreland of central Peru.

Table 1. List of liverwort species identified from bryophyte collections to date in our study area. Numbers in columns refer to number of species collected in a particular habitat, and letter x refers to the presence of epiphyllous taxa found in a given habitat. Habitat typification is as follows: Type 1 (with two subtypes) represents elfin forests on clay, type 2 (with two subtypes) represents elfin forests on sand, type 3 (with two subtypes) represents cloud forests, type 4 represents transitional forest, type 5 represents premontane forest, and type 6 represents lowland forest habitats. Please refer to the following section for further discussion of these habitat types.

Name	1 A	2 A	1 B	2 B	3 A	3 B	4	5	6
Adelanthaceae									
<i>Pseudomarsupidium decipiens</i> (Hook.) Grolle	1	3							
<i>Adelanthus lindenbergianus</i> (Lehm.) Mitt.	1								
Aneuraceae									
<i>Riccardia amazonica</i> (Spruce) Schiffn. ex Gradst.				2					
<i>Riccardia digitiloba</i> (Spruce ex Steph.) Pagán					1				
<i>Riccardia fucioidea</i> (Sw.) Schiffn.	8	4	3	5	3	2			
<i>Riccardia glaziovii</i> (Spruce) Meenks	2	3	1						
<i>Riccardia hymenophytoides</i> (Spruce) Meenks	1								
<i>Riccardia poeppigiana</i> (Lehm. & Lindenb.) Hässel & Meenks		1							
Calyptogeiaceae									
<i>Calyptogea lechleri</i> (Steph.) Steph.					1				
<i>Calyptogea peruviana</i> Nees & Mont.	1			2	2	4			
<i>Mnioloma caespitosum</i> (Spruce) R.M.Schust.				1					
<i>Mnioloma cellulolum</i> (Spreng.) R.M.Schust.	2	2			1	1	2		
<i>Mnioloma cyclostipum</i> (Spruce) R.M.Schust.				3		1			
<i>Mnioloma fissistipulum</i> (Biscl.) R.M.Schust.		1							
<i>Mnioloma venezuelanum</i> (Fulf.) R.M.Schust.				2	2	1			
Cephaloziaceae									
<i>Fuscocephaloziopsis crassifolia</i> (Lindenb. & Gottsche) Váña & Söderstr.	1	1	1	1	2				
<i>Nowellia reedii</i> Robins.		3							
<i>Odontschisma longiflorum</i> (Taylor) Trevis.					1				
<i>Odontschisma cleefii</i> Gradst., S.C. Aranda & Vanderp.	1								
<i>Odontschisma variabile</i> (Lindenb. & Gottsche) Trevis.	1		1	1					

Name	1 A	2 A	1 B	2 B	3 A	3 B	4	5	6
Dumortieraceae									
<i>Dumortiera hirsuta</i> (Sw.) Nees					1				
Herbertaceae									
<i>Triandrophyllum subtrifidum</i> (Hook.f. & Tayl.) Fulf. & Hatch.		1							
Jamesoniellaceae									
<i>Syzygiella perfoliata</i> (Sw.) Spruce			1						
<i>Syzygiella rubricaulis</i> (Nees) Steph.	2	1							
Jubulaceae									
<i>Jubula bogotensis</i> Steph.					4				
Frullaniaceae									
<i>Frullania bicornistipula</i> Spruce		2							
<i>Frullania crispiloba</i> Steph.					x	x			
<i>Frullania ecuadoriensis</i> Steph.		x			x	x			
<i>Frullania griffithiana</i> Gottsche				1	1				
<i>Frullania meridana</i> Steph.			1						
<i>Frullania mirabilis</i> Jack & Steph.	1								
<i>Frullania macrocephala</i> (Lehm. & Lindenb.) Lehm. & Lindenb.						1			
Lejeuneaceae									
<i>Anopolejeunea conferta</i> (Meissn.) A. Evans					1				
<i>Bryopteris filicina</i> (Sw.) Nees					1	1	4		
<i>Ceratolejeunea coarvina</i> (Gottsche) Steph.					1				
<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn.	3	1		3	1	x	x	x	x
<i>Ceratolejeunea fallax</i> (Lehm. & Lindenb.) Bonner					1				
<i>Ceratolejeunea grandiloba</i> J.B. Jack & Steph.	1								
<i>Ceratolejeunea malleigera</i> (Spruce) Steph.					1				
<i>Ceratolejeunea spinosa</i> (Gottsche et al.) Steph.					1				
<i>Cheilejeunea filiformis</i> (Sw.) Ye et al.				2					
<i>Cheilejeunea inflexa</i> (Lehm.) Grolle	2	1	1	2		1			
<i>Cheilejeunea</i> sp. aff. <i>Ch. papillata</i> Solari	1								
<i>Cheilejeunea trifaria</i> (Reinw. & al.) Mizut.					1		1		
<i>Cololejeunea camillii</i> (Lehm.) A. Evans						x		x	
<i>Cololejeunea cardiocarpa</i> (Mont.) A. Evans									x
<i>Cololejeunea erostrata</i> (Herzog) Bernecker & Pócs								x	x
<i>Cololejeunea gracilis</i> (Ast) Pócs						1	2		
<i>Cololejeunea microscopica</i> (Taylor) Schiffn.			x						
<i>Cololejeunea obliqua</i> (Nees & Mont.) Schiffn.									x
<i>Cololejeunea papilliloba</i> (Steph.) Steph.						1			
<i>Cololejeunea papillosa</i> (K.I.Goebel) Mizut.		x				x			
<i>Cololejeunea platyneura</i> (Spruce) A. Evans									x
<i>Cololejeunea sicifolia</i> ssp. <i>jamaicensis</i> (R.M. Schust.) Bernecker & Pócs.							1		
<i>Cololejeunea winkleri</i> (M.I.Morales & Bernecker) Pócs									x
<i>Colura greig-smithii</i> Ast								x	x
<i>Colura tortifolia</i> (Nees & Mont.) Steph.									x
<i>Cyclolejeunea convexistipa</i> (Lehm. & Lindenb.) A. Evans				1	1x	x	x		
<i>Cyclolejeunea peruviana</i> (Lehm. & Lindenb.) A. Evans					x	x	x		
<i>Diplasiolejeunea brunnea</i> Steph.							x		x
<i>Diplasiolejeunea cavifolia</i> Steph.		x			x	x			
<i>Diplasiolejeunea caribea</i> Tixier									
<i>Diplasiolejeunea inermis</i> Tixier					x	x	x	x	
<i>Diplasiolejeunea johnsonii</i> A. Evans						x			
<i>Diplasiolejeunea pauckertii</i> (Nees) Steph.			x						
<i>Diplasiolejeunea pellucida</i> (Meissn.) Schiffn.							x	x	
<i>Diplasiolejeunea</i> sp. nov.		1							
<i>Diplasiolejeunea unidentata</i> (Lehm. & Lindenb.) Schiffn.						x		x	x
<i>Drepanolejeunea anoplantha</i> (Spruce) Steph.					1				
<i>Drepanolejeunea biocellata</i> A. Evans								x	x

Name	1	2	1	2	3	3	4	5	6
	A	A	B	B	A	B			
<i>Drepanolejeunea submuricata</i> R.M. Schust	2	1	1	1					
<i>Drepanolejeunea inchoata</i> (Meissn.) Schiffn.								x	
<i>Drepanolejeunea infundibulata</i> (Spruce) Steph.						x		x	
<i>Drepanolejeunea mosenii</i> (Steph.) Bischler									x
<i>Drepanolejeunea trigonophylla</i> Steph.								x	
<i>Drepanolejeunea</i> sp. nov.	1								
<i>Harpalejeunea cinchonae</i> (Nees) Schiffn.						x		x	
<i>Harpalejeunea tridens</i> (Besch. & Spruce) Steph.						x			x
<i>Lejeunea adpressa</i> Nees						x		x	
<i>Lejeunea sporadica</i> Besch. & Spruce					1				
<i>Lejeunea flava</i> (Sw.) Nees						2	x	x	
<i>Lejeunea grossitexta</i> (Steph.) M.E.Reiner & Goda	1	3							
<i>Lejeunea lusoria</i> (Lindenb. & Gottsche) Steph.						x			
<i>Lejeunea obtusangula</i> Spruce						1			
<i>Lejeunea reflexistipula</i> (Lehm. & Lindenb.) Lehm. & Lindenb.			1						
<i>Lejeunea subspathulata</i> Spruce			1	1					
<i>Leptolejeunea maculata</i> (Mitt.) Schiffn.						x	x	x	x
<i>Leptolejeunea elliptica</i> (Lehm. & Lindenb.) Schiffn.						x		x	x
<i>Lopholejeunea eulopha</i> (Nees) Schiffn.		1		1					
<i>Microlejeunea bullata</i> (Taylor) Steph.						x		x	
<i>Odontolejeunea lunulata</i> (Weber) Schiffn.									x
<i>Prionolejeunea aemula</i> (Gottsche) A.Evans	3	1	1	4	1		1		
<i>Prionolejeunea ampliretis</i> Herzog				1					
<i>Prionolejeunea decora</i> (Taylor) Steph.		1							
<i>Prionolejeunea denticulata</i> (Weber) Schiffn.					1				
<i>Prionolejeunea mucronata</i> (Sande Lac.) Steph.							1		
<i>Prionolejeunea muricatoserrulata</i> (Spruce) Steph.		1					2		
<i>Prionolejeunea scaberula</i> (Spruce) Steph.	1								
<i>Prionolejeunea trachyoides</i> (Spruce) Steph.		1							
<i>Prionolejeunea</i> sp. nov.		1		2					
<i>Stictolejeunea squamata</i> (F. Weber) Schiffn.					2				
<i>Taxilejeunea serpyllifolioides</i> (Raddi) D.P. Costa					1	1			
<i>Xylolejeunea crenata</i> (Nees & Mont.) X.L.He & Grolle					1				
Lepidoziaceae									
<i>Bazzania affinis</i> (Lindenb. & Gottsche) Trevis.		1		2	6	17	1		
<i>Bazzania bidens</i> (Nees) Trevis.	2			1					
<i>Bazzania canelensis</i> (Steph.) Fulford	3		2	2					
<i>Bazzania chilensis</i> (Steph.) Fulford					1				
<i>Bazzania cubensis</i> (Gottsche) Pagán			1		1	1	2		
<i>Bazzania cuneistipula</i> (Gottsche & Lindenb.) Trevis	1	1			1		1		
<i>Bazzania denticulata</i> (Lindenb. & Gottsche) Trevis.		2	1	9	10		1		
<i>Bazzania diversicuspis</i> Spruce						2			
<i>Bazzania falcata</i> (Lindenb.) Trevis.	2								
<i>Bazzania hookeri</i> (Lindenb.) Trevis.	3	8	1	4	2	5	5		
<i>Bazzania jamaicensis</i> (Lehm. & Lindenb.) Trevis.		1		7	3	3			
<i>Bazzania latidens</i> (Gottsche) Fulford		1							
<i>Bazzania longistipula</i> (Nees) Trevis.	2		2			1			
<i>Bazzania pallidivirens</i> (Steph.) Fulford				1		2	2		
<i>Bazzania peruviana</i> (Nees) Trevis.				1					
<i>Bazzania phyllobola</i> Spruce				3	2		5		
<i>Bazzania roraimensis</i> (Steph.) Fulford	8	7	1	3	2		2		
<i>Bazzania serrata</i> Fulford				1			2		
<i>Bazzania stolonifera</i> (Sw.) Trevis.	1						2		
<i>Kurzia capillaris</i> (Sw.) Grolle	2	2	1	4	1				
<i>Lepidozia macrocolea</i> Spruce				1					
<i>Lepidozia cupressina</i> (Sw.) Lindenb.				2			4		
<i>Lepidozia incurvata</i> Lindenb.	5	1	1	4			1		

Name	1 A	2 A	1 B	2 B	3 A	3 B	4	5	6
<i>Lepidozia squarrosa</i> Steph.				2					
<i>Lepidozia subdichotoma</i> Spruce	8	2	3	6					
<i>Micropterygium parvistipulum</i> Spruce				2					
<i>Micropterygium reimersianum</i> Herzog		2				1			
<i>Micropterygium trachyphyllum</i> Reimers					6	6	1		
<i>Mytilopsis albifrons</i> Spruce			2						
<i>Telaranea diacantha</i> (Mont.) J.J.Engel & G.L.Merr.	5	1	1			1			
<i>Telaranea nematodes</i> (Austin) M.A.Howe	1		1		1				
<i>Telaranea</i> sp. 1					1				
<i>Telaranea</i> sp. 2					1				
<i>Zoopsisidella integrifolia</i> (Spruce) R.M.Schust.						1			
Lophocoleaceae									
<i>Cryptolophocolea martiana</i> (Nees) L. Söderstr.					4	10			
<i>Cryptolophocolea martiana</i> var. <i>perissodonta</i> (Spruce) Gradst.					1	3			
<i>Heteroscyphus marginatus</i> (Steph.) Fulford						1			
<i>Leptoscyphus amphibolius</i> (Nees) Grolle						1			
<i>Leptoscyphus gibbosus</i> (Taylor) Mitt.		1							
<i>Leptoscyphus hexagonus</i> (Nees) Grolle	1		1						
<i>Leptoscyphus trapezioides</i> (Mont.) L.Söderstr.		4	1	1	2				
<i>Lophocolea bidentata</i> (L.) Dumort.					1				
<i>Lophocolea muricata</i> (Lehm.) Nees					1				
<i>Lophocolea orbigniana</i> Nees & Mont.		3	3						
Metzgeriaceae									
<i>Metzgeria albinea</i> Spruce	1	8	3	3					
<i>Metzgeria leptoneura</i> Spruce	1			3	1				
Pallaviciniaceae									
<i>Pallavicinia lyellii</i> (Hook) Gray					1	3			
<i>Symphyogyna brongniartii</i> Mont.		2							
<i>Symphyogyna aspera</i> Steph.						1			
Plagiochilaceae									
<i>Plagiochila aerea</i> Tayl.					1				
<i>Plagiochila cristata</i> (Sw.) Lindenb.					1				
<i>Plagiochila deflexirama</i> Taylor					1				
<i>Plagiochila disticha</i> (Lehm.& Lindenb.) Lehm.					1		1		
<i>Plagiochila heterophylla</i> Lindenb. & Lehm.					1				
<i>Plagiochila raddiana</i> Lindenb.					1		1		
<i>Plagiochila rutilans</i> Lindenb.					1				
<i>Plagiochila subplana</i> Lindenb.					1				
<i>Plagiochila superba</i> (Spreng.) Mont. & Nees					1				
Radulaceae									
<i>Radula flaccida</i> Lindenb. & Gottsche								x	
<i>Radula gottscheana</i> Taylor					3	1			
<i>Radula involvens</i> Spruce	2	2							
<i>Radula episcia</i> Spruce							1		
<i>Radula sonsonensis</i> Steph.		1							
<i>Radula javanica</i> Gottsche					1		1		
Scapaniaceae									
<i>Scapania portoricensis</i> Hampe & Gottsche	3	1		9	3				
Trichocoleaceae									
<i>Leomitra flaccida</i> Spruce	1	1	4	1	4				
<i>Trichocolea filicalis</i> Steph.		1							
<i>Trichocolea sprucei</i> Steph.	1	1		5					

Preliminary Habitat Typification

1. Elfin forests on clay

1A. Herbaceous-dominated vegetation type (1950-2100 meters elevation)

On the eastern end of the Ariapo plateau, large sections are devoid of woody vegetation, thus the term elfin forest becomes a bit of a misnomer. This sector might better be characterized as herbaceous-dominated with well-delineated pockets of elfin forest (*Plate I, photos 2 and 5*). Non-woody vascular vegetation here is dominated by the following families and genera- Poaceae (*Neurolepis*), Bromeliaceae (*Pitcairnea, Guzmania, Racinaea*), Orchidaceae (*Epidendrum, Elleanthus, Pleurothallis*), Pteridophyta (*Blechnum, Cyathea*), Asteraceae (*Baccharis, Munnozia, Mikania*), Gentianaceae (*Macrorcarpea, Symbolanthus*), Alstroemeriaceae (*Bomarea*), Liliaceae (*Excremis, Isidrogalvia*), Eriocaulaceae (*Paepalanthus, Syngonanthus*) and Xyridaceae (*Xyris*).

Herbaceous-dominated vegetation types on clay soils were sampled at elevations between 1900 to 2050 meters. The plateau itself undulates quite steeply in places, but the altitudinal variation here is also due to the downward slope of the plateau to the westward in this sector. Vegetation at these sites was entirely herbaceous, with vegetation heights between 5 cm to 1.5 m. All soils were covered by a spongy layer of variously-decomposed material consisting mainly of fine roots, at depths that varied from 5 to 40 cm.

Soils on the poorest sites, vegetatively speaking, have a clear tendency toward waterlogging. Terrestrial lichens, Cyperaceae (*Rhynchopylla, Oreobolus*) and the insectivorous *Drosera* (Droseraceae) are found here, along with the previously-undescribed endemic *Gentiana sirenis* (Gentianaceae). Here, both vegetation height and thickness of organic layer are lowest. Liverwort species (13 families, 24 genera and 41 species) found in this habitat to date include:

**Adelanthus lindenbergianus*

Bazzania bidens

Bazzania canelensis

Bazzania cuneistipula

**Bazzania falcata*

Bazzania hookeri

Bazzania longistipula

Bazzania roraimensis

Bazzania stolonifera

Lepidozia incurvata

Lepidozia subdichotoma

Leptoscyphus hexagonus

Metzgeria albinea

Metzgeria leptoneura

Mnioloma cellulosum

****Odontoschisma cleefii***

Odontoschisma variabile

Prionolejajaeunea aemula

<i>Calypogeia peruviana</i>	* <i>Prionolejeunea scaberula</i>
<i>Ceratolejeunea cornuta</i>	<i>Pseudomarsupidium decipiens</i>
* <i>Ceratolejeunea grandiloba</i>	<i>Radula involvens</i>
<i>Cheilolejeunea inflexa</i>	<i>Riccardia fucoidea</i>
* <i>Cheilolejeunea cf. papillata</i>	<i>Riccardia glaziovii</i>
* <i>Drepanolejeunea sp. nov.</i>	* <i>Riccardia hymenophytoides</i>
<i>Drepanolejeunea submuricata</i>	<i>Scapania portoricensis</i>
* <i>Frullania mirabilis</i>	<i>Syzygiella rubricalus</i>
<i>Fuscocephaloziopsis crassifolia</i>	<i>Telaranea diacantha</i>
<i>Kurzia capillaris</i>	<i>Telaranea nematodes</i>
<i>Lejeunea grossitexta</i>	<i>Trichocolea sprucei</i>
<i>Leomitra flaccida</i>	

*Indicates species found only in this habitat (22% of species identified from this habitat). Boldface indicates new distribution record for Peru (27% of species identified from this habitat).

Where slopes are steepest, sections of vegetation and their underlying layer of variably-decomposed organic material can slip, revealing the bare clay slope beneath. On sites like these, lichens and mosses are typically the first colonizers of the acid clay soils, followed by Orchidaceae, Bromeliaceae and Cyperaceae.

This broad herbaceous-dominated background is broken up especially on sites that are not as prone to water-logging, with mixed herbaceous and small-stature (0.5–1.5 m) woody vegetation. Woody or semi-woody plants commonly encountered intermixed with herbaceous vegetation include Rubiaceae (*Notopleura*), Ericaceae (*Bejaria*, *Disterigma*), Asteraceae (*Baccharis*), Clusiaceae (*Clusia*), Myrsinaceae (*Myrsine*) and Polygalaceae (*Monnina*). Thickness of organic layer capping the soil here has been measured from 50-60 cm, with woody vegetation height up to 2 meters.

On sites with some level of wind-protection, distinct patches of elfin forest with stunted (2-4 meters in height) trees emerge. The majority of bryophytes we encountered in this mixed herbaceous-dominated vegetation were found as epiphytes on woody vegetation, or on the organic layers under the forest canopy. We found liverwort to moss ratios here to be nearly seven to one.

Elfin forest patches in this sector appear from a distance to be relatively homogenous in stature, but on closer inspection the vegetation generally diminishes toward the edge of each patch. Common tree families here include extremely hard-wooded trees, represented by Theaceae, Symplocaceae, Sabiaceae, Myrtaceae,

Melastomataceae, Lauraceae, Annonaceae and Podocarpaceae families, intermixed with smaller tree ferns, *Schefflera* (Araliaceae), *Hedyosmum* (Chloranthaceae) shrubs, and *Geonoma* palms. Mean thickness of the organic layer capping the soil here is slightly above 40 cm. A weak trend toward thinner organic layers with higher stem densities appear in the plot data. Mean canopy height is about 4 meters (*Plate I, photo 4*).

1B. Forest-dominated vegetation type (1850-2000 meters elevation)

Further west (2-3 Km) on the plateau, herbaceous-dominated sectors of vegetation rapidly disappear, becoming a mosaic of near-continuous woodland interspersed with sections of herbaceous-dominated vegetation (*Plate I, photo 6*). Tree heights here are slightly higher than those in the forest patches noted in the herbaceous-dominated vegetation, but never exceed 5 meters, with the exception of the palm *Dictyocaryum lamarckianum*, which can reach up to 7 meters on occasion, emerging above the surrounding canopy to punctuate the skyline.

Species densities can be quite high here- nearly monodominant patches of *Geonoma* palms, with a thick understory of Bromeliads, *Clusia* patches, apparently all the same species, up to about two meters in height, along with large patches of the black-bearded *Euterpe* caatinga palm up to five meters in height are found. Apart from these monodominant patches, the forest matrix itself is also characterized by overall high species densities, with species turnover changing dramatically at the kilometer scale. These elfin forests exhibit a low level of alpha diversity, but a high level of compositional unpredictability, contributing to overall high diversities at the meso-scale. Liverwort species (9 families, 19 genera and 28 species) found in this habitat to date include:

<i>Bazzania canelensis</i>	<i>Lepidozia incurvata</i>
<i>Bazzania cubensis</i>	<i>Lepidozia subdichotoma</i>
<i>Bazzania denticulata</i>	<i>Leptoscyphus hexagonus</i>
<i>Bazzania hookeri</i>	<i>Leptoscyphus trapezioides</i>
<i>Bazzania longistipula</i>	<i>Lophocolea orbigniana</i>
<i>Bazzania roraimensis</i>	<i>Metzgeria albinea</i>
<i>Cheilolejeunea inflexa</i>	<i>*Mytilopsis albifrons</i>
<i>*Cololejeunea microscopica</i>	<i>Odontoschisma variabile</i>
<i>*Diplasiolejeunea pauckertii</i>	<i>Prionolejeunea aemula</i>
<i>Drepanolejeunea submuricata</i>	<i>Riccardia fucoidea</i>
<i>*Frullania meridana</i>	<i>Riccardia glaziovii</i>

Fuscocephaloziopsis crassifolia
Kurzia capillaris
Leomitra flaccida

**Syzygiella perfoliata*
Telaranea diacantha
Telaranea nematodes

*Indicates species found only in this habitat (18% of species identified from this habitat). Boldface indicates new distribution record for Peru (25% of species identified from this habitat).

It should be mentioned here that this habitat type, being located at the outermost section of the transect, has not been as extensively explored as sectors of the transect closer to the river.

2. *Elfin Forests on sand*

2A. Gallery-forest (1800-1900 meters elevation)

Atop the plateau, where the clay soils have been eroded, the underlying quartz-containing sandstone is revealed. Low basins at the base of steep slopes (*Plate II, Photo 8*), as well as very narrow stream valleys (*Plate II, Photo 11*) closely surrounded by steep sandstone cliffs are underlain by a coarse sand substrate.

Tree stature here, in the valleys, on sand, is generally higher than that of adjacent forests on clay. (Mean canopy height is 5.5 m). These gallery forests are protected from the heaviest winds, and due to low water retention on sand, are not prone to waterlogging as are those on the clay soils of the plateau above. In these steep valleys, insolation is lower, humidity is higher, and temperatures are steadier, but lower in the mean than at surrounding plots. Epiphyte volume- dominated by bryophytes - is quite high here (*Plate II, Photo 12*). Mean thickness of organic layer capping the soil is about 40 cm. Interestingly, the presence of standing dead wood (of any appreciable size) is almost nonexistent anywhere on the plateau or in the gallery forests. Any fallen wood (and horizontal trunks) in these gallery forests become rapidly covered by a thick layer of bryophytes and understory plants. In narrow valley bottoms surrounded by steep sandstone cliffs we have found quite a number of well-preserved trunks of very dense wood, recovering them from out of the thick (up to 80 cm) organic layers overlaying the sand. Liverwort species (15 families, 28 genera and 51 species) found in gallery forest on sand substrate to date include:

Bazzania cuneistipula
Bazzania denticulata
Bazzania hookeri
Bazzania jamaicensis

Lopholejeunea eulopha
Metzgeria albinea
Micropterygium reimersianum
Mnioloma cellulolum

<i>*Bazzania latidens</i>	<i>*Mnioloma fissistipulum</i>
<i>Bazzania roraimensis</i>	<i>*Nowellia reedii</i>
<i>Ceratolejeunea cornuta</i>	<i>Prionolejeunea aemula</i>
<i>Cheilolejeunea inflexa</i>	<i>*Prionolejeunea decora</i>
<i>Diplasiolejeunea cavifolia</i>	<i>Prionolejeunea muricatoserrollata</i>
<i>*Diplasiolejeunea replicata</i>	<i>*Prionolejeunea sp. nov.</i>
<i>Drepanolejeunea submuricata</i>	<i>*Prionolejeunea trachyodes</i>
<i>*Frullania bicornistipula</i>	<i>Pseudomarsupidium decipiens</i>
<i>Fuscocephaloziopsis crassifolia</i>	<i>Radula involvens</i>
<i>Kurzia capillaris</i>	<i>*Radula sonsonensis</i>
<i>Lejeunea grossitexta</i>	<i>Riccardia fucoidea</i>
<i>*Lejeunea reflexistipula</i>	<i>Riccardia glaziovii</i>
<i>Lejeunea subspathulata</i>	<i>*Riccardia poeppigiana</i>
<i>Leomitra flaccida</i>	<i>Scapania portoricensis</i>
<i>Lepidozia incurvata</i>	<i>*Symphyogyna brongniartii</i>
<i>Lepidozia subdichotoma</i>	<i>Syzygiella rubricaulis</i>
<i>*Leptoscyphus gibbosus</i>	<i>Telaranea diacantha</i>
<i>Leptoscyphus trapezioides</i>	<i>*Triandrophyllum subtrifidum</i>
<i>Lophocolea orbigniana</i>	<i>*Trichocolea filicaulis</i>
<i>Lopholejeunea eulopha</i>	<i>Trichocolea sprucei</i>
<i>Metzgeria albinea</i>	

*Indicates species found only in this habitat (33% of species identified from this habitat). Boldface indicates new distribution record for Peru (33% of species identified from this habitat).

2B. Steep slopes (1850-2000 meters elevation)

These elfin forests are found entirely downslope from the emergent sandstone cliffs underlying the summit of the Ariapo plateau. The sandy soils found here are eroded entirely from these cliffs. Mean thickness of the organic layer capping the soils here is about 28 cm. Mean canopy height is estimated at 7 meters (*Plate II, photos 7, 10*). Within approximately 250 meters horizontal distance and 150 meters vertical distance from the cliff base, mixed clay/sand soils abruptly replace the pure sand substrate that represents the limit of elfin forest habitat on these steep slopes. On the slopes below this abrupt soil substrate turnover, epiphyte densities are substantially reduced and tree heights increase. Liverwort species (10 families, 22 genera and 44 species represented) found in this habitat to date include:

<i>Bazzania affinis</i>	<i>Lepidozia incurvata</i>
<i>Bazzania bidens</i>	<i>*Lepidozia macrocolea</i>
<i>Bazzania canelensis</i>	<i>*Lepidozia squarrosa</i>
<i>Bazzania denticulata</i>	<i>Lepidozia subdichotoma</i>
<i>Bazzania hookeri</i>	<i>Leptoscyphus trapezioides</i>

<i>Bazzania pallidevirens</i>	<i>Lopholejeunea eulopha</i>
* <i>Bazzania peruviana</i>	<i>Metzgeria albinea</i>
<i>Bazzania phyllobola</i>	<i>Metzgeria leptoneura</i>
<i>Bazzania roraimensis</i>	* <i>Micropterygium parvistipulum</i>
<i>Bazzania serrata</i>	* <i>Mnioloma caespitosum</i>
<i>Calypogeia peruviana</i>	<i>Mnioloma cyclostipum</i>
<i>Ceratolejeunea cornuta</i>	<i>Mnioloma venezuelanum</i>
* <i>Cheilolejeunea filiformis</i>	<i>Odontoschisma variabile</i>
<i>Cheilolejeunea inflexa</i>	<i>Prionolejeunea aemula</i>
<i>Cyclolejeunea convexistipa</i>	* <i>Prionolejeunea ampliretis</i>
<i>Drepanolejeunea submuricata</i>	* <i>Prionolejeunea sp.nov.</i>
<i>Frullania griffithiana</i>	* <i>Riccardia amazonica</i>
<i>Fuscocephaloziopsis crassifolia</i>	<i>Riccardia fucoidea</i>
<i>Kurzia capillaris</i>	<i>Scapania portoricensis</i>
<i>Lejeunea subspathulata</i>	<i>Trichocolea sprucei</i>
<i>Leomitra flaccida</i>	
<i>Lepidozia cupressina</i>	

*Indicates species found only in this habitat (21% of species identified from this habitat). Boldface indicates new distribution record for Peru (29% of species identified from this habitat).

3. Cloud Forest

In the previous section we mentioned the relatively abrupt division found between the cliff-derived coarse sandy soils deposited from above, and the variable loamy clay and sand soil mixtures found downslope. This division of soils represents a break between what we characterize as elfin and cloud forest habitats, occurring in our area at about 1850 meters elevation. Along the steep slopes approaching the Ariapo plateau from the Iparia River valley, tree canopy heights are seen to decrease upslope (see *Figure 6*), reaching an inflection point at this ecotone.

Upper and lower cloud forest are terms of reference we use to distinguish between two easily-identifiable forest types: those with, and those without, a dense but spongy layer of variably-decomposed fine roots overlaying the soil surface. The presence of this layer is diagnostic of what we define as upper cloud forest. Its thickness decreases with altitude until it eventually disappears, at which point lower cloud forest begins. The lower limit of cloud forest we define based on a combination of epiphyte content, the existence of Andean floral (and faunal) elements, and the frequent occurrence of a conspicuous layer of dense, moisture-laden fog moving through the forest. Along the transect, the lower limits of lower cloud forest are

found at about 1250 meters, while those of the upper cloud forest begin around 1600 meters.

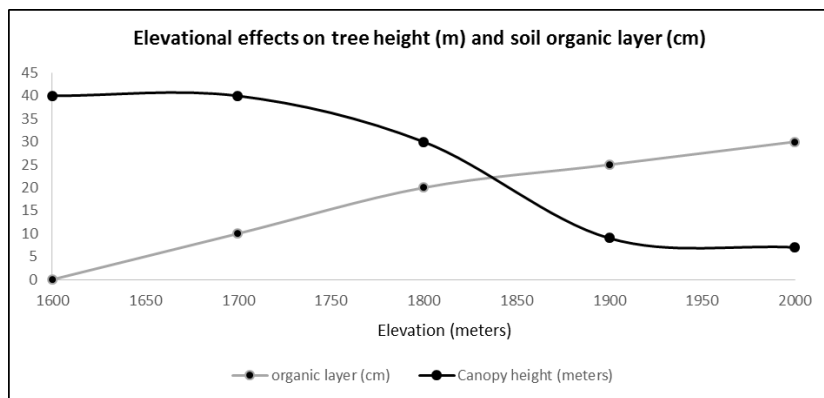


Figure 6. Elevational effects on mean tree canopy height (m) and soil organic layer (cm) between upper cloud forest and elfin forest formations on the steep slopes of the Ariapo uplift.

3A. Upper cloud forest (1850-1950 meters elevation)

The upper cloud forest zone along the transect is, among other emergent landscape elements, characterized by the presence of a persistent organic layer overlaying the soil, and abundant epiphytic vegetation, including bryophytes, pteridophytes, Orchidaceae, Bromeliaceae, Araceae, Piperaceae and a few notable woody epiphytes including *Cybianthus magnus* (Myrsinaceae).

Understory vegetation here is dominated by single-stemmed *Wettinia* and *Geonoma* palms, tree ferns, scandent Cyatheaceae, shrubby Rubiaceae (*Palicourea*, *Psychotria*), abundant viny Ericaceae, and terrestrial Araceae, Gesneriaceae (*Columnea*, *Besleria*) and Alstroemeriaceae (*Bomarea*). Sprawling thickets of the wiry bambusoid grass *Chusquea* increase with elevation.

Mean canopy height here is about 40 meters, while the thickness of the organic layer overlaying the mineral soil decreases with elevation- mean thicknesses measuring about 20 cm. at 1850 meters elevation, becoming gradually reduced in thickness until the organic layer disappears entirely from the soil at about 1600 meters. Large palms, including the rare *Wellfia alfredii* and tall *Dictyocaryum lamarckianum* are quite characteristic of this habitat type, dominating the canopy along with Melastomataceae (*Miconia*) and Clusiaceae (*Clusia*), Lauraceae (*Nectandra*, *Bielschmiedia*), and an

interesting Central American disjunct (*Croizatia*) in the Euphorbiaceae found to be quite common in this habitat (*Plate II, photo 9 and Plate III, photos 15, 16*). Liverwort species (15 families, 33 genera and 66 species represented) found in upper cloud forest habitat to date include:

**Anoplolejeunea conferta*

Bazzania affinis

**Bazzania chilensis*

Bazzania cubensis

Bazzania cuneistipula

Bazzania denticulata

Bazzania hookeri

Bazzania jamaicensis

Bazzania phyllobola

Bazzania roraimensis

Bryopteris filicina

**Calypogeia lechleri*

Calypogeia peruviana

**Ceratolejeunea coarinnata*

Ceratolejeunea cornuta

****Ceratolejeunea fallax***

****Ceratolejeunea malleigera***

**Ceratolejeunea spinosa*

Cheilolejeunea trifaria

Cryptolophocolea martiana

***Cryptolophocolea martiana* var.**

perissodonta

Cyclolejeunea convexistipa

Cyclolejeunea peruviana

Diplasiolejeunea cavifolia

Diplasiolejeunea inermis

**Drepanolejeunea anoplantha*

Prionolejeunea aemula

**Prionolejeunea denticulata*

Radula gottscheana

Radula javanica

****Riccardia digitiloba***

Riccardia fucoidea

Scapania portoricensis

**Dumortiera hirsuta*

Frullania crispiloba

Frullania ecuadoriensis

Frullania griffithiana

Fuscocephaloziopsis crassifolia

**Jubula bogotensis*

Kurzia capillaris

****Lejeunea sporadica***

Leomitra flaccida

Leptoscyphus trapezioides

**Lophocolea bidentata*

**Lophocolea muricata*

Metzgeria leptoneura

Micropterygium trachyphyllum

Mnioloma cellulolum

Mnioloma venezuelanum

**Odontoschisma longiflorum*

Pallavicinia lyellii

**Plagiochila aerea*

**Plagiochila cristata*

**Plagiochila deflexirama*

Plagiochila disticha

**Plagiochila heterophylla*

Plagiochila raddiana

**Plagiochila rutilans*

**Plagiochila subplana*

**Plagiochila superba*

Prionolejeunea aemula

**Prionolejeunea denticulata*

Radula gottscheana

Radula javanica

****Riccardia digitiloba***

Riccardia fucoidea

Scapania portoricensis

**Stictolejeunea squamata*

Taxilejeunea serpyllifolioides

Telaranea nematodes

****Telaranea* sp. 1**

****Telaranea* sp. 2**

****Xylolejeunea crenata***

*Indicates species found only in this habitat (39% of species identified from this habitat). Boldface indicates a new species distribution record for Peru (17% of species identified from this habitat).

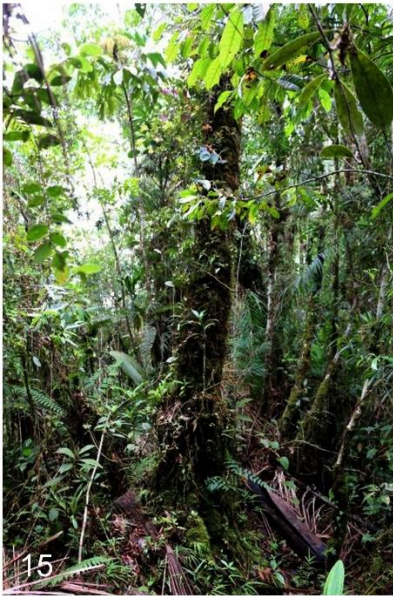


Plate III. Photo 14. View of the Ariapo uplift to the south, from near basecamp along the Iparia River. **Photo 15.** View of interior of lower cloud forest (3B) habitat, on the steep slopes of the Ariapo uplift. **Photo 16.** View of interior of cloud forest at the ecotone (transition) between upper (3A) and lower (3B) cloud forest habitats. **Photo 17.** View of lower cloud forest (3B) habitat descending to the south (Ariapo River drainage) from along narrow ridgetop.

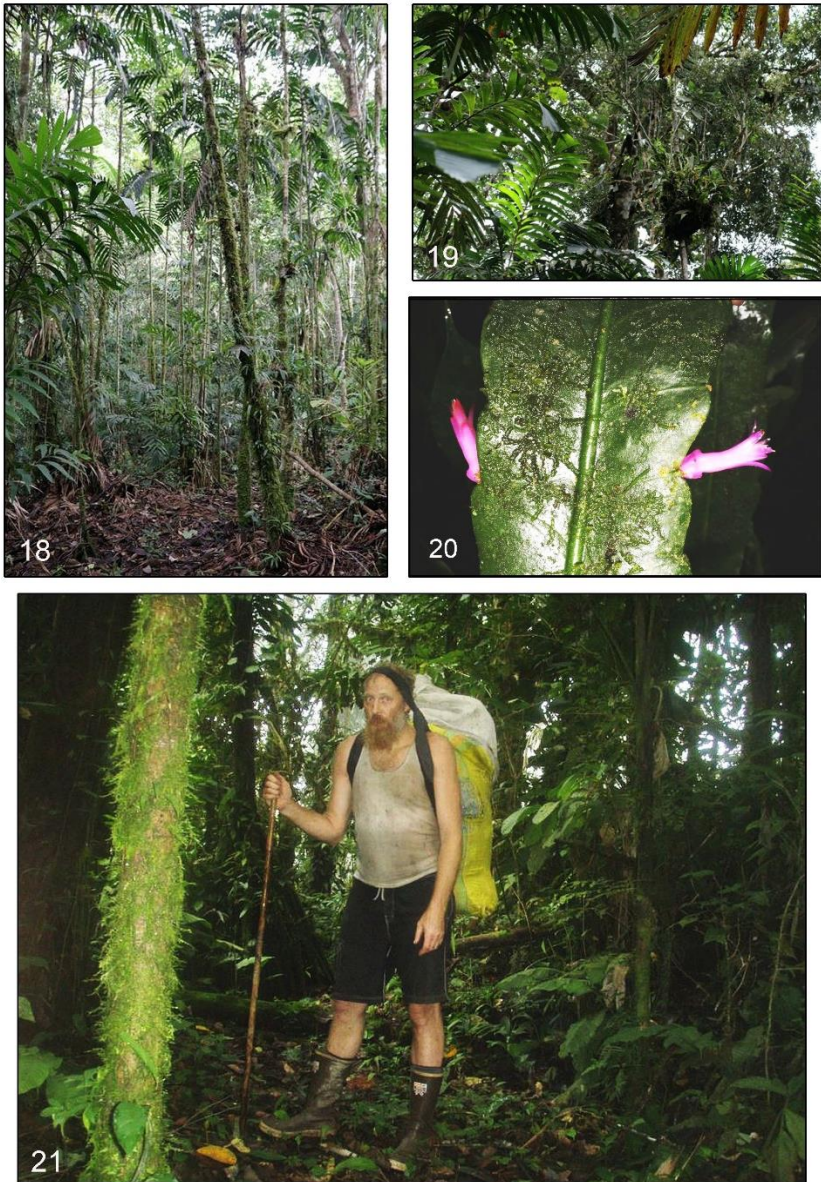


Plate IV. Photo 18. View of interior of lower cloud forest (3B) habitat, showing characteristic *Wettinia augusta* palm understory. **Photo 19.** View of canopy of lower cloud forest (3B) habitat. Woolly monkey visible in center of photo. **Photo 20.** View of epiphyllous liverworts on flowering cactus cladode, transitional forest (4) habitat. **Photo 21.** View of interior of transitional forest (4) habitat.

3B. Lower Cloud forest (1250-1600 meters elevation)

A significant landscape feature of the lower cloud forest zone along the transect is an approximately 2 Km-long narrow ridge running in an east-west direction, climbing from about 1500 to 1600 meters elevation along its length (see *Figure 2*). Along its eastern section, the ridge is dominated by the multiple-trunked *Wettinia augusta* palms (*Plate IV, Photo 18*) that dominate the forest understory along the rocky ridgetop. The westernmost section of the ridge connects directly with the steep slopes and upper cloud forests of the Ariapo uplift, and the first vestiges of soil organic layers so characteristic of upper cloud forests, along with the presence of *Welffia* and *Dictyocaryum* palms, are found here. Cloud forests are also found on the steep, rocky slopes below the ridgeline, descending to merge with transitional forest habitats at about 1250 meters elevation.

Mean canopy height of lower cloud forests is about 30 meters, with mean *Wettinia* palm understory height about 8 meters. The soils along the eastern section of the ridgetop are the least acidic of all soils sampled to date along the transect, although still strongly acidic, with pH values slightly above 5. The very interesting understory vegetation here includes a wide variety of small palms, including *Geonoma*, *Chamedorea*, *Hyospathe* and *Prestoea*, as well as a previously undescribed cauliflorous species of *Brunfelsia* (Solanaceae), numerous shrubs and vines of Ericaceae and Begoniaceae families, abundant epiphytic and terrestrial Araceae, as well as some undescribed large-fruited *Bomarea* (Alstroemeriaceae) species. Epiphylls make up nearly one in four species from our liverwort collections in lower cloud forest, where wind-driven fog and fog precipitation are highest.

Liverwort species (8 families, 26 genera and 49 species represented) found in lower cloud forest habitat to date include the following:

<i>Bazzania affinis</i>	<i>Bazzania longistipula</i>
<i>Bazzania cubensis</i>	<i>Bazzania pallidevirens</i>
* <i>Bazzania diversicuspis</i>	<i>Bryopteris filicina</i>
<i>Bazzania hookeri</i>	<i>Calyptogeia peruviana</i>
<i>Bazzania jamaicensis</i>	<i>Ceratolejeunea cornuta</i>
<i>Cheilolejeunea inflexa</i>	<i>Lejeunea adpressa</i>
<i>Cololejeunea camillii</i>	<i>Lejeunea flava</i>
<i>Cololejeunea gracilis</i>	* <i>Lejeunea lusoria</i>
* <i>Cololejeunea papilliloba</i>	* <i>Lejeunea obtusangula</i>
<i>Cololejeunea papillosa</i>	<i>Leptolejeunea elliptica</i>
<i>Cryptolophocolea martiana</i>	<i>Leptolejeunea maculata</i>
	* <i>Leptoscyphus amphibolius</i>

***Cryptolophocolea martiana* var.
*perissodonta***

Cyclolejeunea convexistipa
Cyclolejeunea peruviana
Diplasiolejeunea cavifolia
Diplasiolejeunea inermis
Diplasiolejeunea johnsonii
Diplasiolejeunea unidentata
Drepanolejeunea infundibulata
Frullania crispiloba
Frullania ecuadoriensis
**Frullania macrocephala*
Harpalejeunea cinchonae
Harpalejeunea tridens
**Heteroscyphus marginatus*

Microlejeunea bullata
Micropterygium reimersianum
Micropterygium trachyphyllum
Mnioloma cellulorum
Mnioloma cyclostipum
Mnioloma venezuelanum
Pallavicinia lyellii
Radula gottscheana
Riccardia fucoidea
**Symphogyna aspera*
Taxilejeunea serpyllifolioides
Telaranea diacantha
**Zoopsidella integrifolia*

*Indicates species found only in this habitat (16% of species identified from this habitat). Boldface indicates new distribution record for Peru (16% of species identified from this habitat).

4. Transitional forest (1000-1250 meters elevation)

Transitional forests represent an interesting ecotone- a transition between the lower elevation premontane forests, with typically Amazonian floral elements, and the increasingly distinct Andean elements found in cloud forest vegetation only a few hundred meters upslope. With higher annual temperatures, these transitional forests receive much lower fog-water precipitation than cloud forest habitats immediately upslope. Even with relatively similar annual rainfall patterns, cloud forests have markedly higher epiphytic density and diversity, cooler temperatures and higher levels of cloud immersion than transitional forest. An elevational profile of the transect as it ascends the Ariapo uplift, with the relative positions of the various habitat types along the slope is illustrated in *Figure 7*.

The mean canopy height of transitional forest along the transect is about 30 meters. Floristic elements that distinguish the transitional forest type from that the premontane forests downslope is the much greater percentage of palms (5% of stems in premontane forest plots vs 25% in transitional forest), as well as the absence of tree ferns in premontane forest plots. This transitional forest type harbors the highest understory bird species diversities and densities along the entire transect (Graham unpublished data).

Liverwort diversity and density declines as one descends from cloud to transitional forest. The abundant liverworts that festoon the

cloud forest in great abundance only a few hundred meters upslope are reduced to discreet patches mainly found on tree trunks and in shady areas near to streams. The majority of our collections here are representatives of the families Lejeuneaceae (mostly epiphylls, see *Plate IV, photo 20*) and Lepidoziaceae. Liverwort species (5 families, 15 genera and 33 species represented) found in transitional forest habitat to date include:

<i>Bazzania affinis</i>	<i>Diplasiolejeunea brunnea</i>
<i>Bazzania cubensis</i>	<i>Diplasiolejeunea inermis</i>
<i>Bazzania cuneistipula</i>	<i>Diplasiolejeunea pellucida</i>
<i>Bazzania denticulata</i>	* <i>Lejeunea flava</i>
<i>Bazzania hookeri</i>	<i>Lepidozia cupressina</i>
<i>Bazzania pallide-virens</i>	<i>Lepidozia incurvata</i>
<i>Bazzania phyllobola</i>	<i>Leptolejeunea maculata</i>
<i>Bazzania roraimensis</i>	<i>Micropterygium trachyphyllum</i>
<i>Bazzania serrata</i>	<i>Mnioloma cellulolum</i>
<i>Bazzania stolonifera</i>	<i>Plagiochila disticha</i>
<i>Bryopteris filicina</i>	<i>Plagiochila raddiana</i>
<i>Ceratolejeunea cornuta</i>	<i>Prionolejeunea aemula</i>
<i>Cheilolejeunea trifaria</i>	* <i>Prionolejeunea mucronata</i>
<i>Cololejeunea gracilis</i>	<i>Prionolejeunea muricatoserrulata</i>
* <i>Cololejeunea sicifolia</i>	* <i>Radula episcia</i>
<i>Cyclolejeunea convexistipa</i>	<i>Radula javanica</i>
<i>Cyclolejeunea peruviana</i>	

*Indicates species found only in this habitat (12% of species identified from this habitat). Boldface indicates new distribution record for Peru (15% of species identified from this habitat).

5. Premontane forest (450-1000 meters elevation)

This forest type covers an elevational range of about 500 meters, and is composed of heterogeneous forests on a variety of substrates. We have conducted soil sampling at four different sites along this section of the transect and found a diversity of soil types and rock formations, including metamorphic flinty rocks at 800-900 meters, a sequence of horizontal bands of emergent karst from 800-600 meters, as well as scattered sandstone formations at about 500 meters elevation.

Mean canopy heights across the elevational range were found to be about 35 meters, with emergent forest giants reaching to over 50 meters in height. Although the forest canopy is higher in premontane forests than other habitat types mentioned above, the understory vegetation is correspondingly much sparser, admitting a greater

amount of light and permitting greater circulation of air, proving a poor habitat for bryophytes to successfully colonize. Liverwort species (2 families, 10 genera, 18 species- all epiphylls) found in premontane forest habitat include:

<i>Ceratolejeunea cornuta</i>	<i>Drepanolejeunea infundibulata</i>
<i>Cololejeunea camillii</i>	* <i>Drepanolejeunea trigonophylla</i>
<i>Cololejeunea erostrata</i>	<i>Harpalejeunea cinchonae</i>
<i>Colura greig-smithii</i>	<i>Lejeunea adpressa</i>
<i>Diplasiolejeunea inermis</i>	<i>Lejeunea flava</i>
<i>Diplasiolejeunea pellucida</i>	<i>Leptolejeunea elliptica</i>
<i>Diplasiolejeunea unidentata</i>	<i>Leptolejeunea maculata</i>
<i>Drepanolejeunea biocellata</i>	<i>Microlejeunea bullata</i>
* <i>Drepanolejeunea inchoata</i>	* <i>Radula flaccida</i>

*Indicates species found only in this habitat

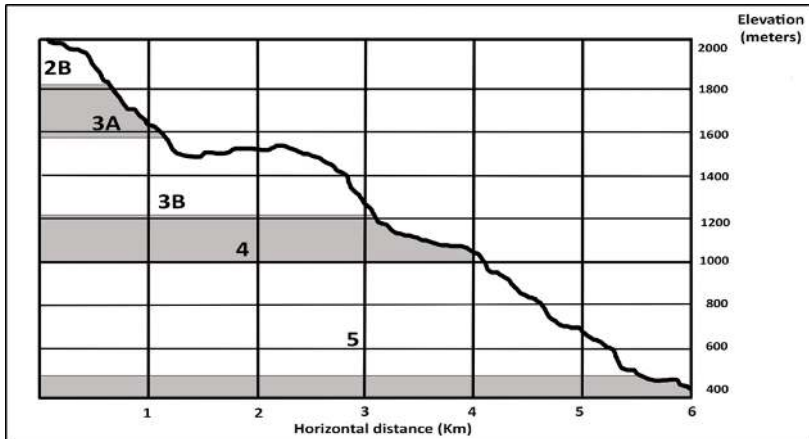


Figure 7. Elevational profile of transect and habitat types on the steep slopes of the Ariapo uplift. 2B. Elfin forest on sand. 3A. Upper cloud forest. 3B. lower cloud forest. 4. Transitional forest. 5. Premontane forest.

6. Lowland forest (200-400 meters elevation)

Lowland forest soils in our study area are, like almost all of the lowland forests in eastern Peru, are the result of deposition of alluvial deposits derived from erosion in the Peruvian Andes during the last glacial cycle. Landforms in the lowlands of our study area consist of low-lying areas prone to seasonal flooding (typically below 200 meters elevation), with scattered low terraces and emergent ridges up to 100 meters higher than the floodplain. Annual rainfalls are lower (see Figure 3), and temperatures higher than

those found in the cordilleran uplift, approximately 10 Km to the west, although as one approaches the uplift, temperatures slightly decrease and rainfall increases. The presence of rocks becomes more prevalent, and the ridges increase gradually in elevation to about 400 meters, where they merge abruptly with the steep slopes of the Ariapo uplift.

While the upland forests of the El Sira Reserved Zone are relatively pristine, adjacent lowland forests have been subject to decades of logging and clearing of forest for subsistence agriculture. Before the advent of mechanized logging in the 1950s, giant mahogany trees (*Swietenia macrophylla*) were a dominant feature on the local landscape, judging by the remnant stumps of this extremely hard-wooded species that still dot the lowland forest floor. Less commercially-viable emergent forest giants still remain in the lowlands, but they are rapidly falling prey to the relentless pressures of resource extraction. Illegal logging remains an existential threat, even inside reserved zones. Unchecked population growth, especially from recent Andean immigrants to the area, results in ever-larger areas of forest cleared for subsistence, and increasingly, commercial agriculture.

Liverwort collections (all epiphylls-16 species from 7 genera, in 1 family) include:

<i>Ceratolejeunea cornuta</i>	<i>Diplasiolejeunea brunnea</i>
* <i>Cololejeunea cardiocarpa</i>	<i>Diplasiolejeunea unidentata</i>
<i>Cololejeunea erostrata</i>	<i>Drepanolejeunea biocellata</i>
* <i>Cololejeunea obliqua</i>	* <i>Drepanolejeunea mosenii</i>
* <i>Cololejeunea platyneura</i>	<i>Harpalejeunea tridens</i>
* <i>Cololejeunea winkleri</i>	<i>Leptolejeunea elliptica</i>
<i>Colura greig-smithii</i>	<i>Leptolejeunea maculata</i>
* <i>Colura tortifolia</i>	<i>Odontolejeunea lunulata</i>

*Indicates species found only in this habitat

Ecological analysis

High rainfall and relatively higher temperatures- along with relative isolation from the main Andean cordillera and a much more recent orogeny- make the El Sira uplift an interesting location to explore patterns of bryophyte distribution and diversity, both at the local scale and within a regional context. The landscapes of the cordillera El Sira present a unique set of characteristics that distinguish it from

other tropical Andean locations, in terms of local ecological gradients as well as endemism.

Figure 8 illustrates the relative diversity of non-epiphyllous liverworts (disregarding habitat 1B which was incompletely sampled, as well as the epiphyllous species from our collections, mostly made in premontane and lowland habitats) between six habitat types, all above 1000 meters of elevation. The accompanying Table 2 outlines the number of species, genera and families found in each habitat type.

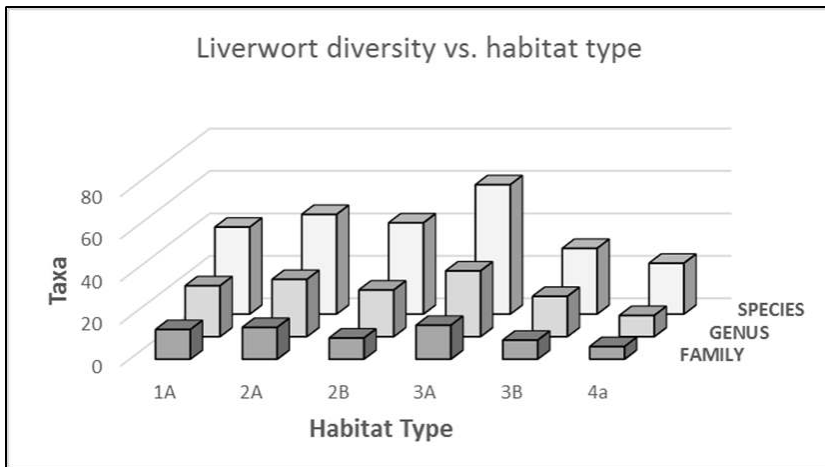


Figure 8. Relative diversity of non-epiphyllous liverwort collections by habitat type: Habitat 1A- 2000 meters elevation; 2A- 1900 m; 3A- 1850-2000 m; 3B- 1600-1850 m; Habitat 4- 1000-1250 m.

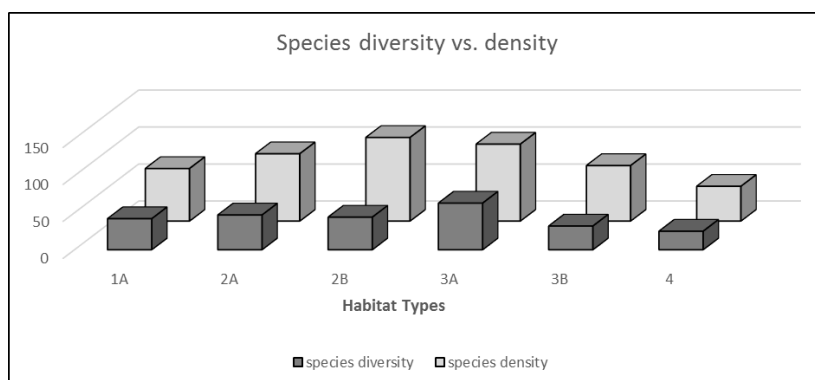
A clear pattern of liverwort diversity diminishing rapidly at lower elevations reveals itself in Table 2, which is typical of other Neotropical elevational inventories of bryophytes in Colombia, Peru, Guyana and French Guiana (Gradstein *et al.* 1995; Gehrig-Downie *et al.* 2013).

In our Figure 8, upper cloud forest (habitat 3A) assumes a position at the apex of the diversity “bump” for species richness per habitat type. Hump-shaped diversity curves along elevational gradients have been reported for a number of organisms in the tropical Andes (Krömer *et al.* 2005), with quite a good deal of variation in inflection point (elevation) depending on the organism in question.

Table 2. A look at non-epiphyllous liverwort diversity between different habitat types.

Habitat	Code	Families	Genera	Species	# Individuals
elfin forest on clay	1A	14	24	41	89
elfin forest on sand (gallery forest)	2A	15	27	47	90
elfin forest on sand (below cliff)	2B	10	22	43	106
upper cloud forest	3A	16	31	61	104
lower cloud forest	3B	9	19	31	78
transitional forest	4	6	10	24	46

In elfin forest on sand substrate on steep slopes (habitat 2B) we find slightly lower overall diversity relative to a smooth curve, but, interestingly, this habitat represents the apex for species densities of bryophytes along the transect, as illustrated in *Figure 9*.

**Figure 9.** Relative diversity and density of non-epiphyllous liverwort collections by habitat type.

What species densities represent in the above graph is a sum of the individual species counts in all collections per habitat, which is a component of diversity that reflects on the heterogeneity of the liverwort community and the equitability of species within it. One aspect of liverwort diversity here, one that remains to be further explored, is the relative abundance of co-occurring species in our collections. Over a third of all macro liverwort collections were found to be composed of mixed species groups. At higher elevations, roughly half of collections contained mixed assemblages of species

with a mean of nearly four species per collection. Interspecific competition among bryophytes in these habitats appears to be minimal, presenting an interesting pattern of bryophyte distribution and diversity at the centimeter-scale. The overall most common species along the transect (see *Table 3*) are well represented among the most common co-occurring species, with a few notable exceptions.

One very interesting aspect of the ecology of the El Sira uplift is the marked downwardly-displaced elevational range of biotic elements found here (in comparison to other ranges throughout the region). A clear pattern of downward displacement of species ranges has been established with regard to both floral as well as faunal (Terborgh 1975) elements, similar to effects seen in the Chocó region of western Colombia (Gentry 1986, Gradstein 1995).

The reasons for this downward biotic displacement are unclear, but theories have been put forward to explain it, including the Massenerhebung effect (Grubb 1971), where the presence of adjacent mountain ranges is theorized to modulate climate with the outcome of raising temperatures due to heat retention and wind shadowing effects. The cordillera El Sira, in the absence of any adjacent mountains thus would be expected to experience a significant lowering of tree line, as well as of species range. The implication of lower temperatures associated with the Massenerhebung phenomenon do not appear to be realized in our study area. In fact, the cordillera El Sira never rises high enough to reach timberline, yet harbors a significant number of montane and sub-alpine bryophyte species.

We can make a rough estimate of floristic similarity between habitat types along the transect using coefficients of biogeographic resemblance, or CBR (Gradstein 1995), in which the number of species in common between two habitats (C) is compared with the total number of species in each of them (N), using the formula $CBR=2C/(N1 + N2)$.

Table 3. Commonest liverwort species identified to date in the El Sira highlands, and commonest species found growing in multi-species assemblages.

COMMONEST SPECIES ALONG TRANSECT		COMMONEST CO-OCCURRING SPECIES	
Family	Name	Family	Name
Aneuraceae	Riccardia fucoidea	Aneuraceae	Riccardia fucoidea
Calypogeiaceae	Calypogeia peruviana	Calypogeiaceae	Calypogeia peruviana
Calypogeiaceae	Mnioloma cellulorum	Lejeuneaceae	Ceratolejeunea cornuta
Lejeuneaceae	Ceratolejeunea cornuta	Lejeuneaceae	Cheilolejeunea inflexa
Lejeuneaceae	Prionolejeunea aemula	Lejeuneaceae	Prionolejeunea aemula
Lepidoziaceae	Bazzania affinis	Lepidoziaceae	Bazzania affinis
Lepidoziaceae	Bazzania denticulata	Lepidoziaceae	Bazzania denticulata
Lepidoziaceae	Bazzania hookeri	Lepidoziaceae	Bazzania hookeri
Lepidoziaceae	Bazzania phyllobola	Lepidoziaceae	Bazzania phyllobola
Lepidoziaceae	Bazzania roraimensis	Lepidoziaceae	Bazzania roraimensis
Lepidoziaceae	Bazzania taleana	Lepidoziaceae	Bazzania wrightii
Lepidoziaceae	Bazzania wrightii	Lepidoziaceae	Kurzia capillaris
Lepidoziaceae	Kurzia capillaris	Lepidoziaceae	Lepidozia incurvata
Lepidoziaceae	Lepidozia incurvata	Lepidoziaceae	Lepidozia subdichotoma
Lepidoziaceae	Lepidozia subdichotoma	Lepidoziaceae	Micropterygium trachyphyllum
Lepidoziaceae	Micropterygium trachyphyllum	Lepidoziaceae	Telaranea diacantha
Lepidoziaceae	Telaranea diacantha	Lophocoleaceae	Cryptolophocolea martiana
Lophocoleaceae	Cryptolophocolea martiana	Metzgeriaceae	Metzgeria albinea
Metzgeriaceae	Metzgeria albinea	Scapaniaceae	Scapania portoricensis
Scapaniaceae	Scapania portoricensis	Trichocoleaceae	Leomitra flaccida

Table 3 summarizes the relative correlation of species found between habitats, with elfin forest sites containing the highest number of species in common and higher divergence between habitats increasing downslope.

Table 4. Liverwort diversity and coefficient of biogeographic resemblance (CBR) observed between different habitat types.

Habitat	families	genera	species	Between habitats	Shared species	CBR (species)
1A	14	24	41			
2A	15	27	47	1A-2A	23	0.52
2B	10	22	43	2A-2B	22	0.49
3A	16	31	61	2B-3A	19	0.37
3B	9	19	31	3A-3B	15	0.33
4	6	10	24	3B-4	8	0.29

The data presented in *Table 4* clearly demonstrate that liverwort assemblages in elfin forest habitats- either on sand or clay substrates- resemble one another much more closely than they do in any non-elfin forest habitats along our transect. The divergence in liverwort communities between elfin and cloud forest habitats (2B-3A) is three times greater than that found between upper and lower

cloud forest (3A-3B) habitats, and between-habitat liverwort community resemblance diminishes even further as elevations decrease.

While a better understanding of emergent elements involved in the complex process of landscape self-organization is one of the stated aims of our investigation, we must acknowledge the time and labor-intensive nature of the effort required to realistically achieve such a goal. The liverwort data we present here are incomplete—several large Neotropical genera, as well as other groups, are poorly represented in our species lists. Neither have we finalized the classification of moss species. Finally, no other organismal data from our collections at the study site, including small mammals, understory birds, amphibians, insects or vascular plants is under consideration in this preliminary exploration of habitat types along our transect. At present, we can only say that, among our zoological collections both bird and bat distributions over the entire elevational gradient—while still incompletely characterized—show clear elevationally-driven diversity differences exist between sampling sites. Interestingly, a small number of bird species are found across all habitats sampled (400–2100 m), while a similarly small fraction of liverwort species can be found across all of our upland (above 1000 m) habitats. There are challenges to the comparison, but both liverworts, bats and birds appear to have a greater potential to disperse across the landscape than more sedentary organisms such as rats and amphibians and vascular plants. Species-level data are not as well characterized for vascular plants, but at the generic level, a clear pattern of separation between elfin and cloud forest genera are noted, with 63% of vascular plant genera unique to elfin forest habitat, 12% unique to cloud forest, and 25% of genera shared between them (N = 175 genera).

This report represents an initial foray into the evaluation of the landscapes and bryoflora of the Selva Central region of Peru. We look forward to further biological exploration and expansion of collection efforts throughout the region. It is expected that the list of known bryophyte species will grow substantially as we continue the taxonomic identification of species from our current collections and expand the regional scope of our collection efforts. These data will serve to better understand longer-range patterns of bryophyte distribution and diversity across the region.

New Distributional Records

A number of new country distribution records have been identified from our liverwort collections. 38 out of the 171 species proved to be new to Peru. This is perhaps not surprising given the relative underrepresentation of Peruvian collections within the context of the tropical Andean bryoflora. The records are considered new to Peru which are not included in the checklist of Menzel (1984) or in the works published after on Peruvian liverworts (Schultze-Motel and Menzel 1987, Inoue 1987, Kürschner and Parolly 1998, Opisso and Churchill 2008, Romanski 2007, Romanski *et al.* 2011, Aranda *et al.* 2014 and in all generic monographs, see below). In addition, in the collection from El Sira there is one *Diplasiolejeunea*, one *Drepanolejeunea* and one *Prionolejeunea* species probably new to science and two unidentified *Telaranea* species, which will be described later.

The signs after each species name (for example 2B) represent the habitats at a certain elevation, where they occur, as described above. After that we give a short account on their general distribution. Some of them are documented by microphotographs. Finally we summarize the ratio of main distribution types among all studied liverworts from El Sira. The nomenclature of species follows Söderström *et al.* 2015 and Söderström *et al.* 2016.

Aneuraceae

Riccardia digitiloba (Spruce ex Steph.) Pagán.

3A. A Neotropical species new to Peru. It has minute thalli with fingerlike upright shoots tipped by gemmae (Gradstein and Costa 2003).

Calypogeiaceae

Mnioloma venezuelanum (Fulford) R.M.Schust. (Plate V, photos 22–25)

2B, 3A, 3B. Hitherto recorded only from Venezuelan Guyana. Its characteristics are the falcate leaves bordered by smaller cells with crenulate margin, orbicular underleaves possessing thick walled cells with large trigones (Fulford 1968, Schuster 1995, 2000).

Cephaloziaceae

Nowellia reedii H.Rob. (Plate VI, photos 28–32)

2A. A species described from Costa Rica, characterized by its reniform, simple leaves with entire dorsal margin and sinus, sometimes interspersed by smaller, bilobed leaves (Robinson 1970). There are even shoots where the bilobed leaves are dominant. As the latter leaf type shows transition to

Nowellia yunckeri Fulford (1968) with shortly bilobed leaves, described from Honduras, it is possible that the two taxa are synonymous. Taking in account the large gap between the Central American and Peruvian occurrences, *Nowellia reedii* might occur also somewhere between the two extremes, just overlooked.

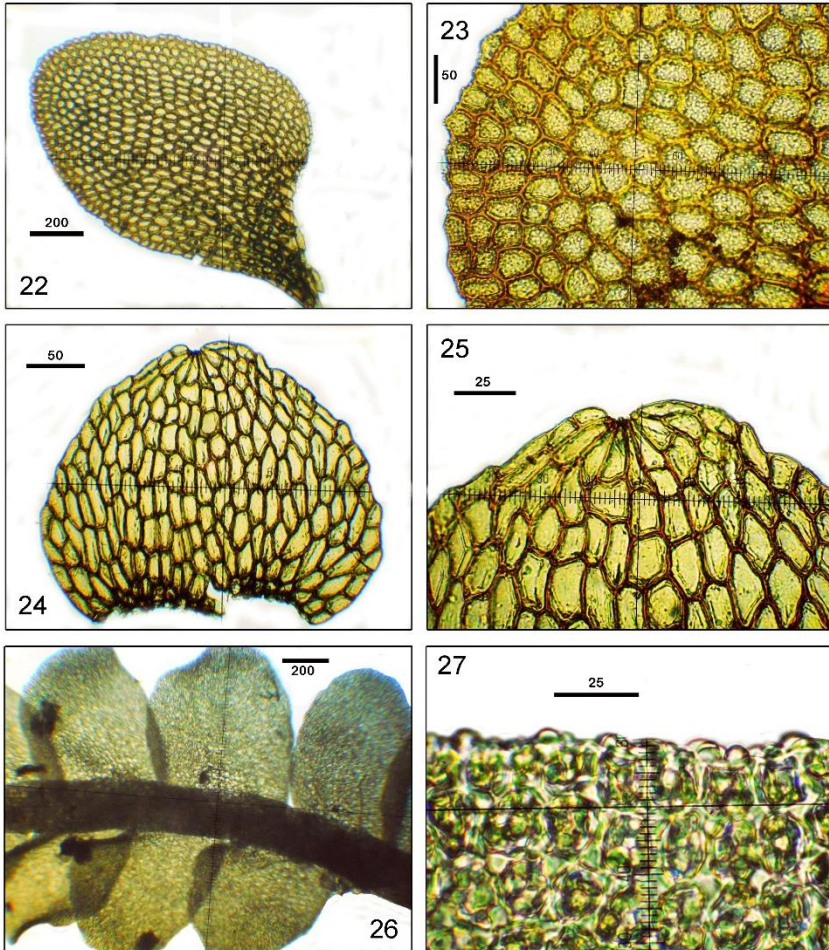


Plate V. Photos 22–25. *Mnioloma venezuelanum* (Fulford) R.M. Schust. from *Graham 6123*. 22: Leaf. 23: Leaf cells near margin. 24: Underleaf. 25: Underleaf apex cells. **Photos 26–27.** *Odontoschisma cleefii* Gradst., Aranda & Vanderp. from *Graham 6229*. 26: Habit, dorsal view. 27: leaf margin cells. (Here and on the further plates all scale bars are indicated in μm).

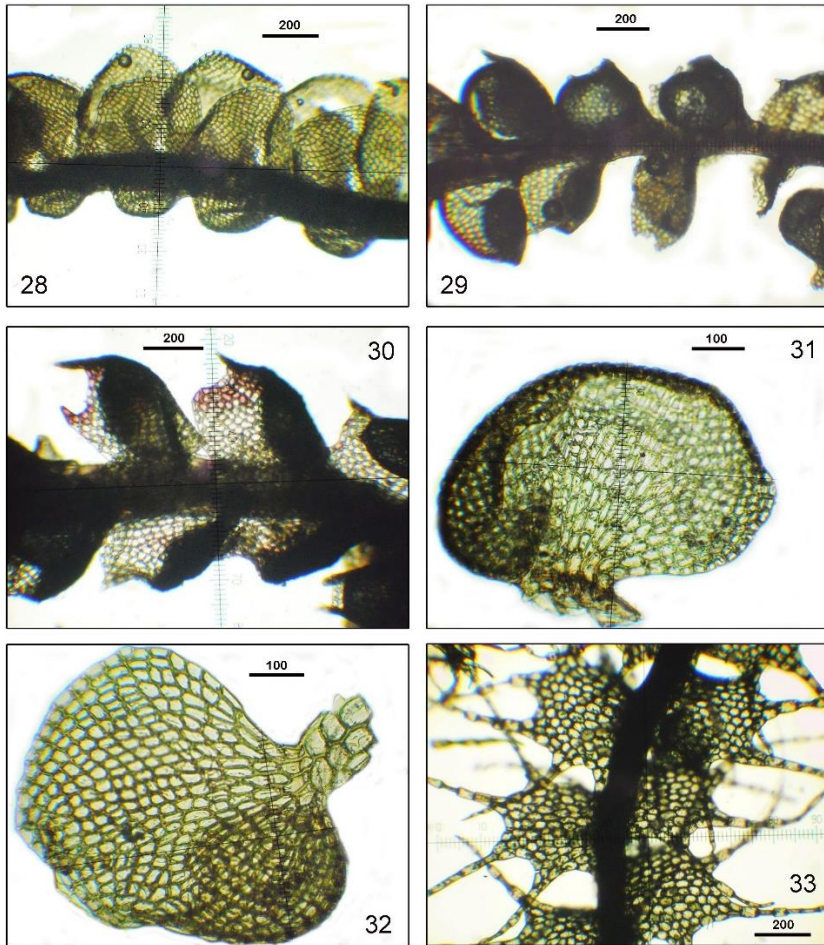


Plate VI. Photos 28–32. *Nowellia reedii* Robins. from *Graham 6594*. 28: Shoot with entire leaves. 29–30: Shoots with bilobed leaves. 30–31: Ventral and dorsal view of the seemingly entire leaves with a small lobe at their base. **Photo 33.** *Lophocolea orbigniana* Nees et Mont. from *Graham 7254*. Shoot, ventral view.

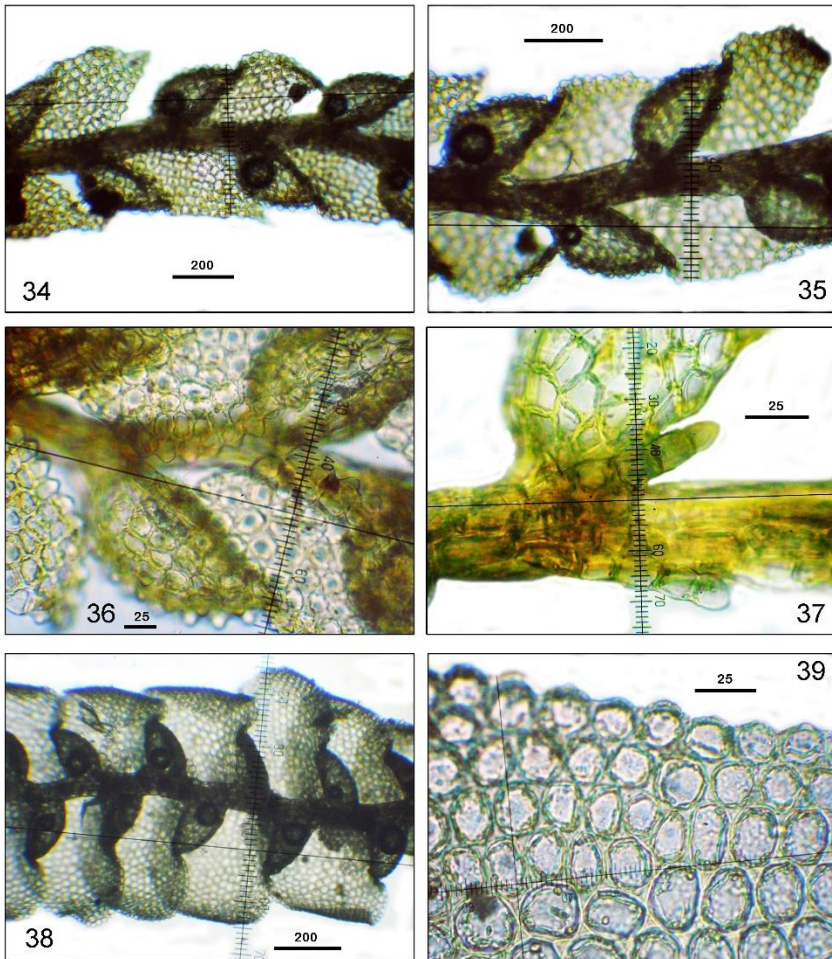


Plate VII. Photos 34–37. *Drepanolejeunea submuricata* R.M. Schust. from *Graham* 6347. 34 and 36: Shoot, dorsal views. 35 and 37: Shoot, ventral views. **Photos 38–39.** *Lejeunea* cf. *sporadica* Besch. & Spruce from *Graham* 6222. 38: Shoot, ventral view. 39: Leaf margin cells.

Odontoschisma* cf. *cleefii Gradst., Aranda & Vanderp. (*Plate V, photos 26–27*)

1A. A species hitherto known only from the páramos of Colombia. It is characterized by the nodulose thickenings of cell walls and large papillae on the cuticle (Aranda *et al.* 2014; Gradstein and Ilkiu-Borges 2015). The Peruvian material deviates by the green color of the plants (S.R. Gradstein, pers. com.).

Frullaniaceae

Frullania griffithsiana Gottsche

2B, 3A. Species known only from Southeast Brazil. Its occurrence in Peru increases the number of the known Andean-SE Brazilian montane disjuncts. It is recognizable from its broad underleaves with wide, obtuse sinus and from its pluriplicate perianth (Stotler 1969, Gradstein and Costa 2003).

Frullania meridana Steph.

1B. A northern Andean endemic previously known from Venezuela, Ecuador and Colombia. The characteristic features are the flat, apiculate leaf apices combined with large, longer than wide, distant underleaves (Stotler 1969, Uribe and Gradstein 1998, Uribe 2004, Schäfer-Verwimp *et al.* 2013).

Lejeuneaceae

Ceratolejeunea fallax (Lehm. & Lindenb.) Bonner

3A. Neotropical species widespread from Mexico and Cuba to Brazil with a very wide altitudinal range. It is similar in many aspects to *C. cornuta* (Lindenb.) Steph. but easily distinguishable in sterile state by its seriate ocelli (Dauphin 2003).

Ceratolejeunea malleigera (Spruce) Steph.

3A. A very rare Andean species known before only from its type described from Bolivia. It is the only species of subgen. *Caduciloba* R.M. Schust. in the Neotropics with scattered ocelli. Also unique by its perianths with two bulbous horns (Dauphin 2003, Gradstein *et al.* 2003). Its relationship to the African *Ceratolejeunea papuliflora* Steph. is to be clarified (Pócs 2011).

Cheilolejeunea inflexa (Lehm.) Grolle

1A, 1B, 2A, 2B. Scattered Neotropical species known from Costa-Rica throughout the Andes to Brazil (Morales 1991, Gradstein and Costa 2003, Dauphin 2005). The large rounded papillae on the sharp pointed leaves are its characteristic properties.

Cheilolejeunea* sp. aff. *Cheilolejeunea papillata Solari (*Plate X, photos 54–56*)

1A. *Cheilolejeunea papillata* is an Andopatagonian species, known from Chile (Valdivia, Magellanes). The strongly thickened, confluent trigones and large papillae of the acute leaves and the obtusely rounded underleaf lobes are properties of the species (Solari 1981, 1983), but the underleaf lobes of Peruvian specimen are much broader than those of the type, maybe representing a new taxon (S.R. Gradstein pers. com.).

Cololejeunea gracilis (Ast) Pócs

3B, 4. A widespread Neotropical epiphyllous species. Occurs mostly as var. ***linearifolia*** (R.M. Schust.) Pócs, with very narrow, only 2 cells wide reduced leaves (Pócs *et al.* 2014).

Cololejeunea papilliloba (Steph.) Steph.

3B. Widespread Neotropical epiphyllous species distributed from Mexico to Brazil. Characteristic are the uniform, ellipsoid-ovate leaves of each cell with a round papilla and its lobule 2/3 of the lobe length (Pócs and Bernecker 2009, Pócs *et al.* 2014).

Cololejeunea sicifolia (Gottsche ex A.Evans) Pócs & Bernecker ssp. ***jamaicensis*** (R.M. Schust.) Bernecker & Pócs

4. Widespread Neotropical epiphyllous species distributed from Mexico to Brazil. It has lanceolate leaves ending in uniseriate apex. The two lobule teeth are equal and parallel. Its ssp. *jamaicensis* has acutely papillose lobe cells and occurs mostly in montane areas (Pócs *et al.* 2014).

Diplasiolejeunea johnsonii A.Evans

3B. Central-American–Caribbean species known in the Andes only from Ecuador. Characteristic is by its strongly involuted lobule having teeth with superimposed cells. The lobule is often continued into involute lobe margin. Underleaf apex broadly rounded (Reyes 1982, Schäfer-Verwimp 2004).

Drepanolejeunea submuricata R.M. Schust. (*Plate VII, photos 34–37*)

1A, 1B, 2A, 2B. A species described from Dominica from the Lesser Antilles. The strongly papillose lanceolate leaves remind *Drepanolejeunea granatensis* (Jack. et Steph.) Bischler (Bischler 1964), but the Peruvian specimens have much narrower underleaf lobes, only 1–2 cells wide at their base (Schuster 1996). The occurrence in the Peruvian Andes extends much its known distribution.

Lejeunea sporadica Besch. & Spruce (*Plate VII, photos 38–39*)

Syn.: *Crossotolejeunea parva* Steph. (Schäfer-Verwimp 2010)

3A. Widespread Caribbean species (from Honduras through the Antilles to Guyana) with questionable occurrence in the Northern Andes. As the Peruvian specimen sterile, we cannot confirm its Andean distribution with safety (Reiner-Drehwald and Goda 2000).

Lejeunea isocalycina (Nees) Steph.

3B. Neotropical species relatively rare in the Andes. Large species with very large, cordate underleaves and eplicate, terete perianth (Gradstein and Costa 2003).

Lejeunea subspathulata Spruce (*Plate VIII, photo 40–41*)

Syn.: *Echinocolea subspathulata* (Spruce) Grolle

2A, 2B. A widely distributed and very variable Caribbean-Andean species, occurring also in SE-Brazil at different elevations. The leaves are ovato-falcate with rounded apex, mammillose only in their upper half (Ilkiu-Borges 2005a).

Priornolejeunea ampliretis Herzog (*Plate VIII, photos 42–43*)

2B. Caribbean-Northern Andean species characterized by its irregularly dentate leaf margins with larger and smaller teeth and slightly obcordate perianths (Ilkiu-Borges 2006).

Prionolejeunea decora (Taylor) Steph. (*Plate VIII, photos 44–45*)

2A. Caribbean-Central American-Andean species. The new Peruvian locality extended its known distribution southwards. It has caducous leaves and obovate perianth with ciliate marginal laciniae over more than half of perianth length (Ilkiu-Borges 2006).

Prionolejeunea mucronata (Sande Lac.) Steph.

4. Northern Andean-Caribbean species occurring also in SE Brazil. All leaf lobe cells possess small papillae restricted to the center of their surface (Ilkiu-Borges 2006).

Prionolejeunea trachyodes (Spruce) Steph. (*Plate IX, photos 46–47*)

2A. Distributed in the northern part of South America + Dominica. Its occurrence in Peru is its southernmost extension. It is characterized by the large papillae on each lobe and lobule cells occupying almost the whole surface (Ilkiu-Borges 2006).

Xylolejeunea crenata (Nees & Mont.) X.L.He & Grolle

3A. Lowland species often on decaying wood throughout the Neotropics. 2-3 large ocelli in transversal row + scattered ocelli and narrow underleaf about 1.5 stem width are typical (Gradstein and Ilkiu-Borges 2009).

Lepidoziaceae

Bazzania canelensis (Steph.) Fulford (*Plate IX, photos 48–51*)

1A, 1B, 2B. Northern Andean species not yet known from Peru. Leaves without prominent teeth, underleaves large, suborbicular, entire, with auriculate base (Fulford 1962).

Bazzania cuneistipula (Gottsche) Lindenb. & Trevis. (*Plate X, photos 52–53*)

1A, 2A, 3A, 4. Widespread Neotropical species of relatively low altitudes. Small plants with obtusely bidentate leaves, cells with large trigones. Underleaves slightly 4-lobed (Bernecker-Lücking 1999). Trigones normally small in *B. cuneistipula*; large trigones are characteristic of *B. roraimensis*, which is doubtfully distinct from *B. cuneistipula* and might be a phenotype of the latter sp. from high elevation (S.R. Gradstein, pers. com.). The distinguishing characters between the two are not clear (Fulford 1962), as the cell size is small (up to 20 µm) combined with the large trigones in the Peruvian specimens.

Lepidozia squarrosa Steph.

2B. Centro-American -Andean species. Small size plant. Its distant squarrouse spreading leaves have straight lobes (Fulford 1966).

Lepidozia subdichotoma Spruce

1A, 1B, 2A, 2B. North Andean species not yet known from Peru. Filiform, laxly branching species with denuded appearance. The leaves and underleaves not wider than the stem and closely appressed to it (Fulford 1966).

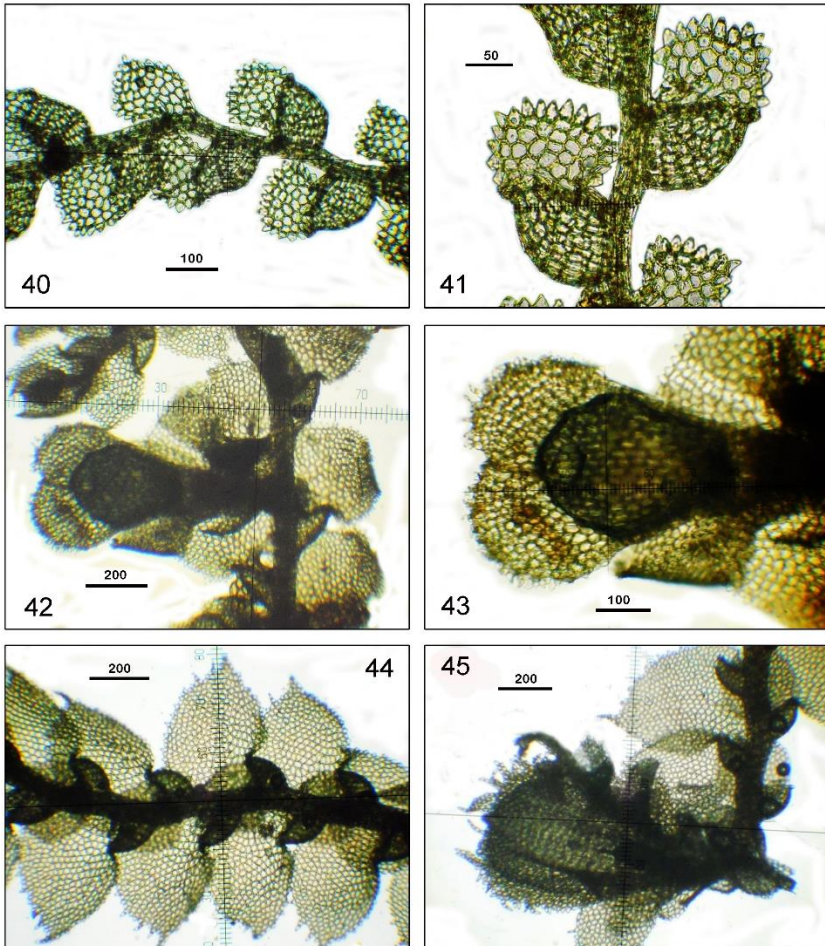


Plate VIII. Photos 40–41. *Lejeunea subspathulata* Spruce from Graham 6314. 40: Shoot, ventral view. 41: Shoot, dorsal view. **Photos 42–43.** *Prionolejeunea ampliretis* Herzog from Graham 6202. 42: Shoot, ventral view. 43: Perianth, ventral view. **Photos 44–45.** *Prionolejeunea decora* (Taylor) Steph. 44: Shoot, ventral view. 45: Perianth, ventral view.

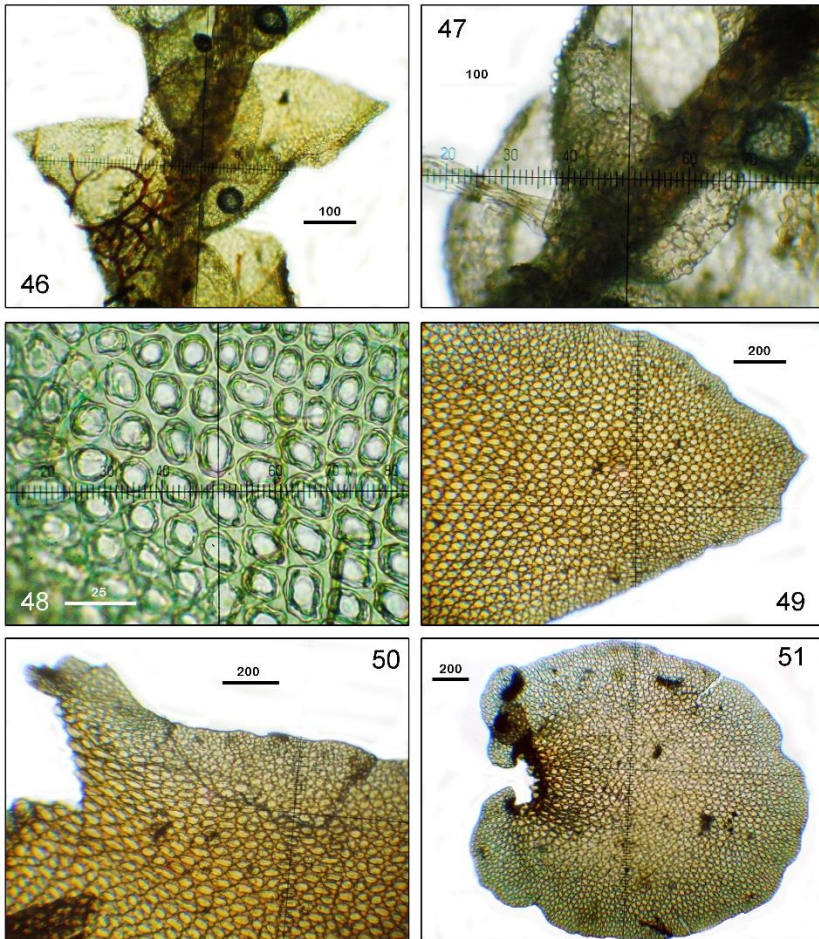


Plate IX. Photos 46–48. *Prionolejeunea trachyoides* (Spruce) Steph. from *Graham 6388*. 46: Shoot, ventral view. 47: Lobule with papillae, ventral view. 48: Median leaf cells with large papillae. **Photos 49–51.** *Bazzania canelensis* (Steph.) Fulford. from *Graham 6623*. 49: Leaf apex. 50: Postical leaf base. 51: Underleaf.

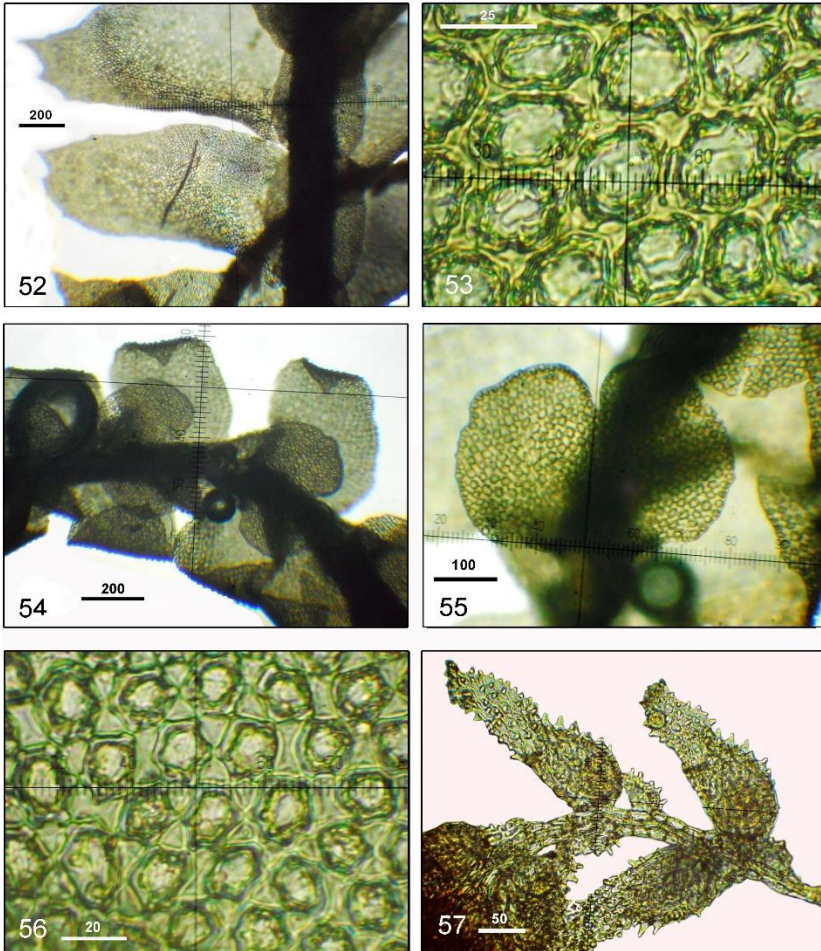


Plate X. Photos 52–53. *Bazzania cuneistipula* (Gottsche & Lindenb.) Trevis. from Graham 5496/B. 52: Shoot, ventral view. 53: Median leaf cells. **Photos 54–56.** *Cheilolejeunea* sp. aff. *Cheilolejeunea papillata* Solari from Graham 5407. 54: Habit, ventral view. 55: Underleaf. 56: Median lobe cells. **Photo 57.** *Cololejeunea sicifolia* ssp. *jamaicensis* (R.M. Schust.) Bernecker & Pócs, from Graham 5592. Habit, dorsal view.

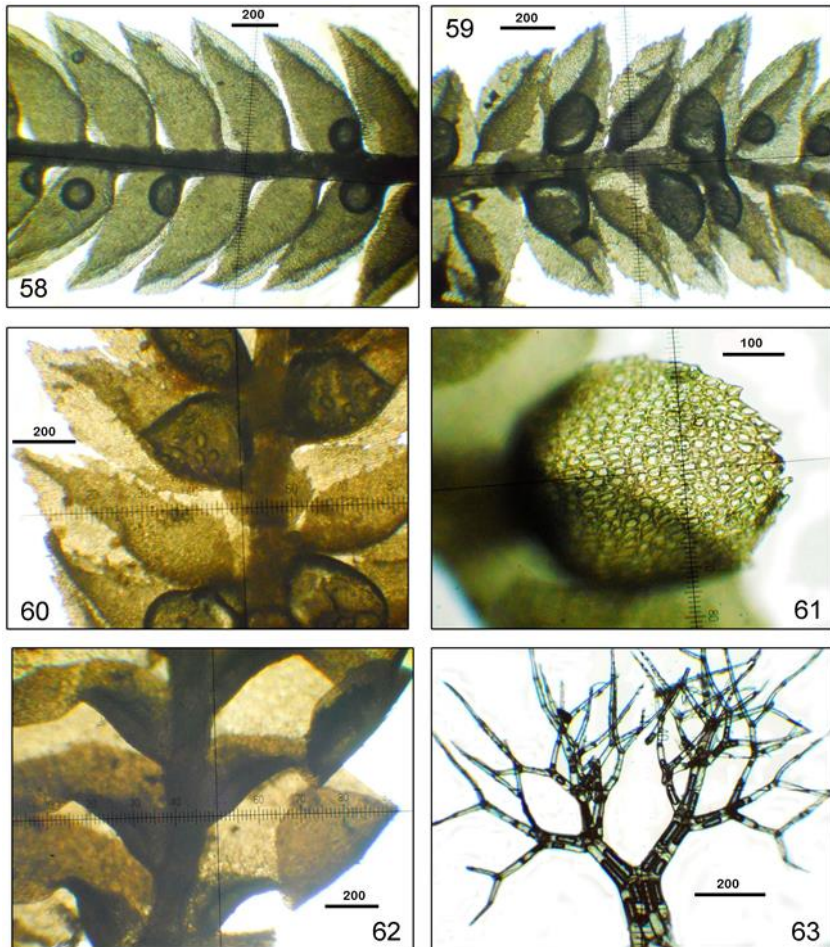


Plate XI. Photo 58. *Micropterygium parvistipulum* Spruce from *Graham 6204*, shoot ventral view. **Photo 59–61.** *Micropterygium reimersianum* Herzog from *Graham 6590*. 59 and 60: Shoot, ventral view. 61: Underleaf. **Photo 62.** *Radula involvens* Spruce from *Graham 6332*, shoot, ventral view. **Photo 63.** *Trichocolea sprucei* Steph. from *Graham 6152/B*, stem leaf, ventral view.

***Micropterygium parvistipulum* Spruce (Plate XI, photo 58)**

2B. Amazonian species of lowland rainforest habitats, new to Peru. The leaves convex with mammillose projection, having long, toothed wings. The underleaves decreasing in size towards the stem apex (Fulford 1966).

***Micropterygium reimersianum* Herzog (Plate XI, photos 59–61)**

2A. Andean – SE Brazilian montane species with shortly ovate, concave leaves without protrusions on the cells. Underleaves large, suborbicular, not decreasing in size towards stem apex (Fulford 1966). The Peruvian

specimens agree with the type except, that the leaves are not shortly ovate but much longer and narrower lanceolate.

Telaranea diacantha (Mont.) J.J.Engel & G.L.Merr.

1A, 1B, 2A, 3B. Bicontinental species occurring in the tropics of America and Africa. The uniseriate segments of bilobed leaves are only 4–6 cells long, 16–24 µm in diameter and not collapsing when dry (Engel 2004).

Lophocoleaceae

Lophocolea orbigniana Nees et Mont. (*Plate VI, photo 33*)

1B, 2A. Andean altimontane species known from Bolivia and Ecuador. Tiny, brownish plant with orbicular leaves surrounded by long ciliae. Underleaves much dissected, spider like (Fulford 1976, Gradstein *et al.* 2003). Probably is only a phenotype with cilia all around the leaves and with a striate-papillose cuticle of *Leptoscyphus trapezoides* (Mont.) L.Soderstr. (S.R. Gradstein, pers. com.).

Cryptolophocolea martiana var. ***perissodonta*** (Spruce) Gradst.

3A, 3B. Neotropical variety of a bicontinental Afro-American species. It differs from *C. martiana* having 1–2 teeth also on its ventral margin (Gradstein and Costa 2003).

Plagiochilaceae

Plagiochila rutilans Lindenb.

3A. Caribbean-Andean-SE Brazilian species. Apart from the parallel sided, horizontally spreading, narrowly oblong leaves with subisodiametric cells, the best character is the strong peppermint smell of the plant when fresh or in not too old herbarium specimens (Huneck *et al.* 1984, Heinrichs *et al.* 2001, Gradstein 2016).

Plagiochila raddiana Lindenb.

3A. Widespread throughout the Neotropics, from southern USA to Bolivia. The ventral leaf bases are entire, longly decurrent and usually amplate, and branching mostly terminal (Heinrich and Gradstein 2000, Gradstein 2016).

Radulaceae

Radula involvens Spruce (*Plate XI, photo 62*)

1A, 2A. A species of the northern Andes and Guyana. Relatively large, brown pigmented, hanging epiphyte with strongly falcate leaves and narrowly inflated, incurved lobule. Leaf cells with bulging trigones (Castle 1959, Yamada 1980).

Radula sonsonensis Steph.

2A. Typical for high altitude subpáramo and páramo habitats, previously known only from several places in Colombia. Yellowish green plant with strongly concave leaves mammillose on their dorsal surface (Castle 1963, Jans 1979, Uribe and Gradstein 1998).

Trichocoleaceae

***Trichocolea filicaulis* Steph.**

2A. North Andean-Caribbean species. Tiny, slightly branching, without paraphyllia, usually intermixed among other bryophytes. Leaves only with three segments (Fulford 1962, Schuster 2000).

***Trichocolea sprucei* Steph. (Plate XI, photo 63)**

1A, 2A, 2B. Andean-Caribbean species. 1.2 mm broad, pinnate, tuft-forming shoots with quadrifid (bisbifid) leaves (Fulford 1962, Schuster 2000).

Phytogeographical Evaluation of Liverwort Records

The amount of species recorded for the Cordillera El Sira, while still incomplete, is sufficient to establish phytogeographical relationships for the majority of liverworts identified in the study area (see *Figure 10*). There remain a few species which are difficult to incorporate into any of the distribution types outlined below. As would be expected from its location, the Cordillera El Sira possesses a considerable number of Andean endemics, although the ratio of Andean endemics here is less than found in Columbian or Ecuadorian páramos. Some connections are found also with Ando-Patagonian species, which in southernmost South America occur near sea level, but are found to occur at increasingly higher elevations as their distribution extends northward.

It is interesting to note that the number of Afro-American bicontinental species is much higher than those of Asian-American joint distribution. We find similarly in Asian areas many Afro-Asian bicontinental species but very few American conspecifics. This probably can be explained both by the ancient direct land connection between South America and Africa and by the much greater distance between Asia and the Americas for long range air dispersal.

Andean endemics (16 species)

The distribution of these species is restricted to the tropical Andes, especially to their northern and wetter sections. In the study area, these same species tend to be restricted to the cloud forest and elfin forest belts above 1500 m. Their number is most probably limited due to the fact that real páramo vegetation, which tends to be richest in endemics, does not occur in the Cordillera El Sira.

Bazzania canelensis, *Bazzania serrata*, *Ceratolejeunea grandiloba*, *Ceratolejeunea malleigera*, *Drepanolejeunea* sp. nov., *Frullania meridana*, *Lepidozia subdichotoma*, *Leptoscyphus hexagonus*,

Lophocolea orbigniana, *Mnioloma fissistipulum*, *Mnioloma venezuelanum*, *Odontoschisma cleefii*, *Prionolejeunea* sp. nov., *Radula involvens*, *Radula episcia*, *Radula sonsonensis*.

Ando – Caribbean (16 species)

These species are not restricted to the tropical Andes (mostly its northern section), but are found to be widespread in the Caribbean. These do not appear to be limited altitudinally.

Bazzania bidens, *Bazzania cubensis*, *Ceratolejeunea spinosa*, *Drepanolejeunea submuricata*, *Drepanolejeunea trigonophylla*, *Jubula bogotensis*, *Lejeunea sporadica*, *Leptoscyphus amphibolius*, *Lejeunea subspathulata*, *Micropterygium trachyphyllum*, *Prionolejeunea ampliretis*, *Prionolejeunea decora*, *Prionolejeunea mucronata*, *Riccardia hymenophytoides*, *Riccardia poeppigiana*, *Trichocolea filicaulis*.

Ando – Patagonian (4 species)

These species extend their distribution to the southern temperate Andes and Patagonia. Again, more of them occur in the higher parts of the Andes, with páramo vegetation.

Bazzania chilensis, *Bazzania peruviana*, *Prionolejeunea scaberula*, *Triandrophyllum subtrifidum*.

Ando – Amazonian (2 species)

These species occur also in Amazonia or on Roraima in the Guyana Highlands.

Bazzania phyllobola, *Micropterygium parvistipulum*.

Ando – Brazilian (5 species)

Montane species which sporadically occur also in southeastern Brazil.

Bazzania pallidevirens, *Frullania griffithiana*, *Heteroscyphus marginatus*, *Lejeunea grossitexta*, *Lepidozia incurvata* (+ Mesoamerica).

North Andean – Mesoamerican (7 species)

The species which extends their distribution from the northern Andes to the cordilleras of Central America, but are not known from the Caribbean Islands.

Frullania bicornistipula, *Frullania mirabilis*, *Lepidozia squarrosa*, *Nowellia reedii*, *Plagiochila deflexirama*, *Plagiochila heterophylla* (+ Atlantic part of Europe), *Prionolejeunea muricatoserrulata*.

Northern South American (4 species)

These species are distributed in the northern part of tropical South America.

Bazzania diversicuspis, *Micropterygium reimersianum*, *Prionolejeunea trachyoides*, *Zoopsidella integrifolia* (+ Caribbean Islands).

Neotropical (82 species)

The bulk of investigated taxa. These are very widespread all over the Neotropics or scattered at least in three major regions of the American tropics between Mexico and SE Brazil. Most of them have wide ecological tolerance but some of them are restricted to mountainous areas with higher altitudes.

Anoplolejeunea conferta, *Bazzania affinis*, *Bazzania cuneistipula*, *Bazzania denticulata* (montane), *Bazzania falcata*, *Bazzania hookeri*, *Bazzania jamaicensis*, *Bazzania latidens*, *Bazzania longistipula*, *Bazzania roraimensis* (montane), *Bazzania stolonifera*, *Bryopteris filicina*, *Calypogeia lechleri*, *Ceratolejeunea fallax*, *Cheilolejeunea inflexa*, *Cololejeunea camillii*, *Cololejeunea erostrata*, *Cololejeunea gracilis*, *Cololejeunea papilliloba*, *Cololejeunea sicifolia*, *Cololejeunea winkleri*, *Colura greig-smithii*, *Colura tortifolia*, *Cyclolejeunea convexistipa*, *Cyclolejeunea peruviana*, *Diplasiolejeunea brunnea*, *Diplasiolejeunea caribea*, *Diplasiolejeunea inermis*, *Diplasiolejeunea pauckertii* (montane), *Diplasiolejeunea pellucida*, *Diplasiolejeunea replicata*, *Drepanolejeunea anoplantha* (montane), *Drepanolejeunea biocellata*, *Drepanolejeunea inchoata* (montane), *Drepanolejeunea infundibulata*, *Drepanolejeunea mosenii*, *Frullania crispiloba*, *Frullania ecuadoriensis*, *Frullania mucronata*, *Fuscocephaloziopsis crassifolia* (+ Atlantic part of Europe), *Harpalejeunea tridens*, *Harpalejeunea cinchonae*, *Heteroscyphus gibbosus* (montane), *Syzygiella rubricaulis* (+ Azores), *Leiomitra flaccida*, *Lejeunea adpressa*, *Lejeunea lusoria*, *Lejeunea obtusangula*, *Lejeunea reflexistipula*, *Lepidozia macrocolea* (montane), *Leptolejeunea elliptica*, *Leptoscyphus trapezioides*, *Microlejeunea bullata*, *Microlejeunea bullata*, *Mnioloma cellulolum*, *Mnioloma cyclostipum*, *Mytilopsis albifrons*, *Odontoschisma longiflorum*, *Plagiochila aerea*,

Plagiochila cristata, *Plagiochila disticha*, *Plagiochila raddiana*, *Plagiochila rutilans* (montane), *Plagiochila subplana*, *Plagiochila superba*, *Prionolejeunea aemula*, *Prionolejeunea denticulata*, *Radula gottscheana*, *Radula mexicana*, *Radula javanica*, *Riccardia digitiloba*, *Riccardia fucoidea*, *Riccardia glaziovii* (montane), *Scapania portoricensis*, *Stictolejeunea squamata*, *Symphyogyna aspera*, *Symphyogyna brogniartii*, *Syzygiella perfoliata*, *Taxilejeunea serpyllifolioides*, *Trichocolea sprucei*, *Xylolejeunea crenata*.

Amero-African (16 species)

The American-African bicontinental species were summarized and mapped first by Gradstein *et al.* (1983). This time 41 species in 8 genera were classified in this group of distribution. After 30 years they were reinvestigated (Gradstein *et al.* 2013) and the floristic and taxonomic research since has raised their number to 74 species in 13 genera. From our area the *Pseudomarsupidium decipiens* (+ Atlantic Europe), *Calypogeia peruviana*, *Adelanthus lindenbergianus* (+ Atl. Eur.), *Ceratolejeunea coarina*, *Ceratolejeunea cornuta*, *Cololejeunea microscopica* (+ Atl. Eur.), *Cryptolophocolea martiana*, *Kurzia capillaris*, *Lepidozia cupressina*, *Mnioloma caespitosum*, *Odontolejeunea lunulata*, *Odontoschisma variabile*, *Radula flaccida*, *Riccardia amazonica*, *Telaranea diacantha*, *Telaranea nematodes*.

Amero-Asian bicontinental (1 species)

In contrast to the previous group, only one species can be classified here: *Cololejeunea papillosa*.

Pantropical (12 species)

The species belong here, which occur at least on the three greater tropical continents or on their surrounding islands. They are usually common species of widespread distribution. Although less than half of the species in the Cordillera El Sira belong to *Lejeuneaceae* family, the majority of this group belongs here. *Lejeuneaceae* are not known for their good spore survival ability (Zanten and Gradstein 1988). In their case probably vegetative diaspores (gemmae, shoot and leaf fragments) play a more important role in their long range air dispersal, a subject in need of further investigation (Zanten and Pócs 1981).

Cheilolejeunea trifaria, *Cololejeunea cardiocarpa*. *Cololejeunea obliqua*. *Cololejeunea platyneura*, *Diplasiolejeunea cavifolia*,

Diplasiolejeunea unidentata, *Lejeunea flava*, *Leptolejeunea maculata*, *Lopholejeunea eulopha*, *Metzgeria albinea*, *Metzgeria leptoneura*, *Pallavicinia lyellii* (+ warm temperate).

Subcosmopolite (3 species)

Dumortiera hirsuta (Oceanic), *Lophocolea bidentata*, *Lophocolea muricata* (Oceanic).

Unknown (3 species)

Cheilolejeunea sp. aff. *Ch. papillata*, *Telaranea* sp. 1, *Telaranea* sp. 2.

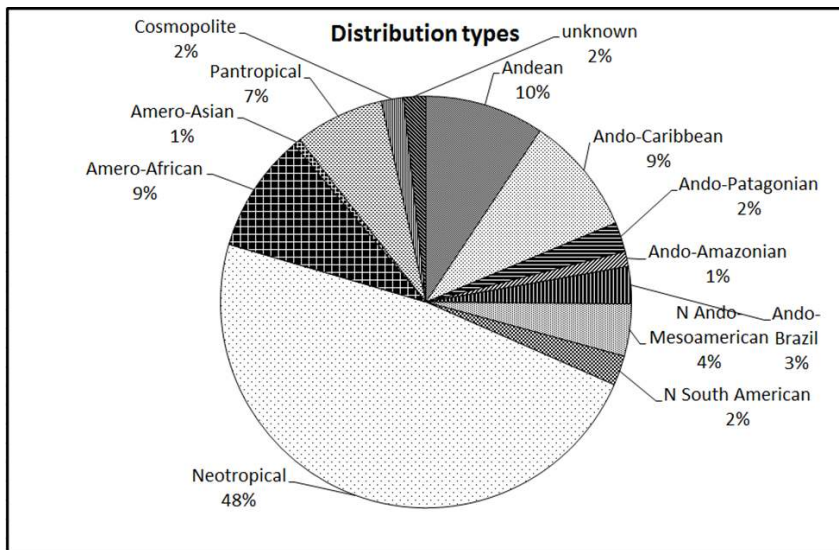


Figure 10. The ratio of the different distribution types in the investigated El Sira area.

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REFERENCES

- ARANDA, S.C., GRADSTEIN, S.R., PATIÑO, J., LAENEN, B., DÉSAMORÉ, A. & VANDERPOORTEN, A. (2014). Phylogeny, classification and species delimitation in the liverwort genus *Odontoschisma* (Cephaloziaceae). *Taxon* **63**(5): 1008–1025.
- BERNECKER-LÜCKING, A. (1999). Key to the Latin American species of *Bazzania* S.F. Gray. *Tropical Bryology* **16**: 117–126.
- BISCHLER, H. (1964). Le genre *Drepanolejeunea* Steph. en Amérique Centrale et Méridionale. *Revue Bryologique et Lichénologique* **34**: 15–179.
- CASTLE, H. (1959). A revision of the genus *Radula*. Part II. Subgenus *Acroradula*. Section 3. *Dichotomae*. *Journal of the Hattori Botanical Laboratory* **21**: 1–52.
- CASTLE, H. (1963). A revision of the genus *Radula*. Part II. Subgenus *Acroradula*. Section 6. *Saccatae*. *Revue Bryologique et Lichénologique* **32**: 1–48.
- CHURCHILL, S., BALSLEV, H., FORERO, E. & LUTEY, J.L. (eds., 1995). *Biodiversity and conservation of Neotropical montane forests*. New York Botanical Garden, Bronx, N.Y.
- DAUPHIN, G. (2003). *Ceratolejeunea*. New York Botanical Garden, Bronx. *Flora Neotropica monograph* **90**: 1–87.
- DAUPHIN, G. (2005). Catalogue of Costa Rican Hepaticae. *Tropical Bryology* **26**: 141–218.
- ENGEL, J.J. & MERRILL, G.L.S. (2004). Austral Hepaticae. 35. A taxonomic and phylogenetic study of *Telaranea* (Lepidoziaceae), with a monograph of the genus in temperate Australasia and commentary on extra-Australasian taxa. *Fieldiana* **44**: 1–265.
- FRAHM, J.-P. & GRADSTEIN, S.R. (1991). An altitudinal zonation of tropical rain forests using bryophytes. *Journal of Biogeography* **18**: 669–678.
- FULFORD, M.H. (“1962”, 1963). Manual of the leafy Hepaticae of Latin America, Part I. *Memoirs of the New York Botanical Garden* **11**: 1–172.
- FULFORD, M.H. (1966). Manual of the leafy Hepaticae of Latin America, Part II. *Memoirs of the New York Botanical Garden* **11**(2):173–276.
- FULFORD, M.H. (1968). Manual of the leafy Hepaticae of Latin America, Part III. *Memoirs of the New York Botanical Garden* **11**(3):277–392.

- FULFORD, M.H. (1976). Manual of the leafy Hepaticae of Latin America, Part IV. *Memoirs of the New York Botanical Garden* **11**(4):393–535.
- GEHRIG-DOWNIE, C., OBREGON, A., BENDIX, J. & GRADSTEIN, R. (2013). Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *Journal of Bryology* **35**: 243–254.
- GENTRY, A.H. (1986). Species richness and floristic composition of Choco region plant communities. *Caldasia* **15**: 71–91.
- GRADSTEIN, S.R. (1995). Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. In: CHURCHILL, S. P. et al. (eds.), *Biodiversity and Conservation of Neotropical Montane Forests*, New York Botanical Garden, Bronx, N.Y., pp. 321–334.
- GRADSTEIN, S.R. (2013). Afro-American hepatics revisited. *Polish Botanical Journal* **58**(1): 149–177.
- GRADSTEIN, S.R. (2016). The genus *Plagiochila* (Marchantiophyta) in Colombia. *Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales* **40**(154): 104–136.
- GRADSTEIN, S.R. & COSTA, D.P. (2003). The Hepaticae and Anthocerotae of Brazil. *Memoirs of the New York Botanical Garden* **87**: 1–317.
- GRADSTEIN, S.R. & FRAHM, J.-P. (1987). Die floristische Höhengliederung der Moose entlang des BRYOTROP-Transsektes in NO-Peru. In W. FREY (ed.): *Moosflora und -vegetation in Regenwäldern NO-Perus. Ergebnisse der Bryotrop-Expedition nach Peru 1982. Beihefte zur Nova Hedwigia* **88**: 105–113.
- GRADSTEIN, S.R. & ILKIU-BORGES, A.L. (2009). Guide to the plants of Central French Guyana Part 4. Liverworts and Hornworts. *Memoirs of the New York Botanical Garden* **76**: 1–144.
- GRADSTEIN S.R., & ILKIU-BORGES A.L. (2014). A taxonomic revision of the genus *Odontoschisma* (Marchantiophyta: Cephaloziaceae). *Nova Hedwigia* **100**(1/2): 15–100.
- GRADSTEIN, S.R., MENESES, R.I.Q. & ARBE, B.A. (2003). Catalogue of the Hepaticae and Anthocerotae of Bolivia. *Journal of the Hattori Botanical Laboratory* **93**: 1–67.
- GRADSTEIN, S.R. & PÓCS, T. (1989). *Bryophytes*. In: LIETH, H. & WERGER, M.J.A. (eds.), *Tropical Rain Forest Ecosystems*. Elsevier, Amsterdam.
- GRADSTEIN, S.R., PÓCS, T. & VÁÑA, J. (1983). Disjunct Hepaticae in Tropical America and Africa. *Acta Botanica Academiae Scientiarum Hungaricae* **29**: 127–171.
- GRADSTEIN, S.R. & URIBE-M.J. (2016). *Marchantiophyta*. In: BERNAL, R., GRADSTEIN, S.R. & CELIS, M. (eds.) *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia Press, Bogotá, pp. 282–352.
- GRUBB, P. J. (1971). Interpretation of the 'Massenerhebung' effect on tropical mountains. *Nature* **229**: 44–45.
- HEINRICHS, J. (2002). A taxonomic revision of *Plagiochila* sect. *Hylacoetes*, sect. *Adiantoidaeae* and sect. *Fuscoluteae* in the Neotropics with a preliminary subdivision of Neotropical Plagiochilaceae into nine lineages. *Bryophyt. Biblioth.* **58**: 1–183.
- HEINRICHS, J. & GRADSTEIN, S.R. (2000). A revision of *Plagiochila* sect. *Crispatae* and sect. *Hypnoides* (Hepaticae) in the Neotropics. I. *Plagiochila disticha*, *P. montagnei* and *P. raddiana*. *Nova Hedwigia* **70**: 161–184.
- HEINRICHS, J., GROTH, H. & GRADSTEIN, S. R. (2001). *Plagiochila rutilans* (Hepaticae): A poorly known species from Tropical America. *The Bryologist* **104**(2): 350–361.

- HUNECK, S., CONNOLLY, J.D., HARRISON, L.J., JOSEPH, R.S.I. & PÓCS, T. (1984). 1-(3,4-Dihydroxy-5-methoxyphenyl)-3-methylbut-2-ene from the liverwort *Plagiochila rutilans*. *Phytochemistry* **23**: 2396–2397.
- ILKIU-BORGES, A.L. (2005a). A taxonomic revision of *Echinocolea* (Lejeuneaceae, Hepaticae). *Nova Hedwigia* **80**(1-2): 45–71.
- ILKIU-BORGES, A.L. (2006). *A taxonomic monograph of the genus Prionolejeunea (Lejeuneaceae, Jungermanniopsida)*. Cuvillier Verlag, Göttingen, 190 pp.
- INOUE, H. (1987). *Studies on oil bodies of some Peruvian hepatics*. In: H. INOUE (ed.): *Studies on cryptogams in Southern Peru*. Tokai University Press, pp. 75–94.
- INOUE, H. (1987). *Notes on the Plagiochilaceae XIV. New species of Plagiochila (Dum.) Dum. from the Neotropics*. In H. INOUE (ed.): *Studies on cryptogams in Southern Peru*. Tokai University Press, pp. 97–105.
- JANS, E. (1979). *Studies on Colombian cryptogams VI. High Andean species of Radula (Hepaticae)*. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. C, **82**(4): 421–432.
- JOVET-AST, S. (1948). Hépatiques des Antilles françaises récoltées par P. et V. Allorge en 1936. II. *Revue Bryologique et Lichénologique* **17**: 24–34.
- KRÖMER, T., KESSLER, M., GRADSTEIN, S.R. & ACEBEY, A. (2005). Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography* **32**(10): 1799–1809.
- KÜRSCHNER, H. & PAROLLY, G. (1998). Stammepiphytische Moosgesellschaften am Andenostabhang und im Amazonas-Tiefland von Nord-Peru. *Nova Hedwigia* **66**(1-2): 1–87.
- LEON-YANEZ, S., GRADSTEIN, S.R. & WEGNER, C. (2006). *Hepáticas (Marchantiophyta) y Antoceros (Anthocerotophyta) del Ecuador*. Publicaciones del Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito.
- MENZEL, M. (1984). Katalog der Lebermoose von Peru, 1. *Willdenowia* **14**: 473–523.
- MORALES, Z.M. (1991). Las hepáticas comunicadas para Costa Rica. *Tropical Bryology* **4**: 25–57.
- OPISSO, J.M. & CHURCHILL, S.P. (2008). Bryophytes from the environs of Yanachaga-Chemillén National Park, Department of Pasco, Peru. *The Bryologist* **111**: 310–317.
- PÓCS, T. (1977). Bioclimatic studies in the Uluguru Mountains (Tanzania, East Africa) II. Correlations between orography, climate and vegetation. *Acta Botanica Academiae Scientiarum Hungaricae* **22**: 163–183.
- PÓCS, T. (1980). The epiphytic biomass and its effect on the water balance in two rainforest types in the Uluguru mountains. *Acta Botanica Academiae Scientiarum Hungaricae* **26**: 143–167.
- PÓCS, T. (1994). The altitudinal distribution of Kilimanjaro bryophytes. In: SEYANI & CHIKUNI (eds.), *Proceedings of the XIII Plenary Meeting AETFAT, Malawi* **2**: 797–812.
- PÓCS, T. (2011). East African Bryophytes XXIX. The *Ceratolejeunea* (Lejeuneaceae) species in the Indian Ocean islands. *Polish Botanical Journal* **56**(2): 131–153.
- PÓCS, T. & BERNECKER, A. (2009). Overview of *Aphanolejeunea* (Jungermanniopsida) after 25 years. *Polish Botanical Journal* **54**(1): 1–11.
- PÓCS, T., BERNECKER, A. & TIXIER, P.† (2014). Synopsis and key to species of Neotropical *Cololejeunea* (Lejeuneaceae). *Acta Botanica Hungarica* **56**(1-2): 185–226.

- REINER-DREHWALD, M.E. & GODA, A. (2000). Revision of the genus *Crossotolejeunea* (Lejeuneaceae, Hepaticae). *Journal of the Hattori Botanical Laboratory* **89**: 1–54.
- REYES, D.M. ("1982" 1983). El género *Diplasiolejeunea* en Cuba. *Acta Botanica Academiae Scientiarum Hungaricae* **28**: 145–180.
- ROBINSON, H. (1970). Notes on the genus *Nowellia*. *The Bryologist* **73**: 150–152.
- ROMANSKI, J. (2007). *Epiphytic bryophytes and habitat microclimate variation in lower montane rainforest, Peru*. 146 pp. (A thesis submitted in partial fulfilment of the requirements for an Honours Degree at the School of Geography and Environmental Studies, University of Tasmania.) <http://eprints.utas.edu.au/17171/2/Whole-Romanski-thesis-2013.pdf>
- ROMANSKI, J., PHARO, E.J., & KIRKPATRICK, J.B. (2011). Epiphytic bryophytes and habitat variation in montane rainforest, Peru. *The Bryologist* **114**(4): 720–731.
- SCHÄFER-VERWIMP, A. (2004). The genus *Diplasiolejeunea* (Lejeuneaceae, Marchantiopsida) in the Tropical Andes, with description of two new species. *Cryptogamie, Bryologie* **25**(1): 3–17.
- SCHÄFER-VERWIMP, A. (2010). A checklist of the liverworts and hornworts of Dominica, West Indies. *Cryptogamie, Bryologie* **31**(4): 313–415.
- SCHÄFER-VERWIMP, A., LEHNERT, M. & NEBEL, M. (2013). Contribution to the knowledge of the bryophyte flora of Ecuador. *Phytotaxa* **128**(1): 1–63.
- SCHULZE-MOTEL, W. & MENZEL, M. (1987). Die Lebermoosflora im BRYOTROP-Transect von Peru. In: FREY, W. (ed.): Moosflora und -vegetation in Regenwäldern NO-Perus. Ergebnisse der Bryotrop-Expedition nach Peru 1982. *Beihefte zur Nova Hedwigia* **88**: 61–104.
- SCHUSTER, R.M. (1995). Phylogenetic and taxonomic studies of Jungermanniidae, III. Calypogeiaceae. *Fragmenta Floristica et Geobotanica* **40**: 825–888.
- SCHUSTER, R.M. (1996). Studies on Lejeuneaceae II. Neotropical taxa of *Drepanolejeunea* (Spr.) Schiffn. *Nova Hedwigia* **62**(1/2): 1–46.
- SCHUSTER, R.M. (2000). Austral Hepaticae. Part 1. *Beihefte zur Nova Hedwigia* **118**: 1–524.
- SOLARI, S.S. (1981). Miscelánea Briológica (Hepaticae), IV. Novedades en Lejeuneaceae. *Comunicaciones del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia", Botánica* **2**(11): 67–75.
- SOLARI, S.S. (1983). Lejeuneaceae. Catálogo de especies Andinopatagónicas. *Journal of Hattori Botanical Laboratory* **54**: 533–553.
- SÖDERSTRÖM, L., BARRIE, F.R., HAGBORG, A., CRANDALL-STOTLER, B.J., GRADSTEIN, S.R., STOTLER, R.E.† & VON KONRAT, M. (2015). Notes on Early Land Plants Today. 73. Genera of Lejeuneaceae established in the period 1884–1893: dates of validation and implications. *Phytotaxa* **220**(2): 143–198.
- SÖDERSTRÖM, L., HAGBORG, A., VON KONRAT, M., BARTHOLOMEW-BEGAN, S., BELL, D., BRISCOE, L., BROWN, E.†, CARGILL, D.C., COOPER, E.D., COSTA, D.P., CRANDALL-STOTLER, B.J., DAUPHIN, G., ENGEL, J.J., FELDBERG, K., GLENNY, D., GRADSTEIN, S.R., HE, X., HEINRICH, J., HENTSCHEL, J., ILKIU-BORGES, A.L., KATAGIRI, T., KONSTANTINOVA, N.A., LARRAÍN, J., LONG, D.G., NEBEL, M., PÓCS, T., PUCHE, F., REINER-DREHWALD, E., RENNER, M.A.M., SASS-GYARMATI, A., SCHÄFER-VERWIMP, A., SEGARRA MORAGUES, J.G., STOTLER, R.E.†, SUKKHARAK, P., THIERS, B.M., URIBE, J., VAÑA, J., VILLARREAL, J.C., WIGGINTON, M., ZHANG, L. & ZHU, R-L. (2016). World checklist of hornworts and liverworts. *PhytoKeys* **59**: 1–828.

- STOTLER, R.E. (1969). The genus *Frullania* subgenus *Frullania* in Latin America. *Nova Hedwigia* **18**: 397–555.
- TERBORGH, J. & WESKE, J. (1975). The Role of Competition in the Distribution of Andean Birds. *Ecology* **56**(3): 562–576.
- URIBE, J.M. (2004). Estudios en ejemplares tipo del género *Frullania*. III. Sobre *F. meridana* Steph. y *F. setigera* Steph. (Jubulaceae-Hepaticae). *Tropical Bryology* **25**: 29–34.
- URIBE, J.M. & GRADSTEIN, S.R. (1998). Catalogue of the Hepaticae and Anthocerotae of Colombia. *Bryophytorum Bibliotheca* **53**: 1–99.
- YAMADA, K. (1980). Notes on type specimens of *Radula* taxa from Latin America (1). *Journal of the Hattori Botanical Laboratory* **48**: 243–257.
- ZANTEN, B.O. van & GRADSTEIN, S.R. (1988). Experimental dispersal geography of Neotropical liverworts. *Beiheft zur Nova Hedwigia* **90**: 41–94.
- ZANTEN, B.O. van & PÓCS, T. (1981). Distribution and dispersal of bryophytes. *Advances in Bryology* **1**: 479–562.

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