
BRYOFLORA AND LANDSCAPES OF THE EASTERN ANDES OF CENTRAL PERU:

I. LIVERWORTS OF THE EL SIRA COMMUNAL RESERVE

James G. Graham^{1,2}, *Margaux Fischer*³ & *Tamás Pócs*^{4*}

^{1,3}Field Museum, 1400 S. Lake Shore Drive, Chicago IL 60605 USA, E-mail: jgraham@fieldmuseum.org; ²Herbario Forestal, Universidad Nacional Agraria La Molina, Avenida La Universidad, Lima, Perú; E-mail: fischer.margaux@gmail.com;

⁴Institute of Biology, Eszterházy Károly University, P.O. Box 43., Eger, H-3301, Hungary; *E-mail: colura@upcmail.hu

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.

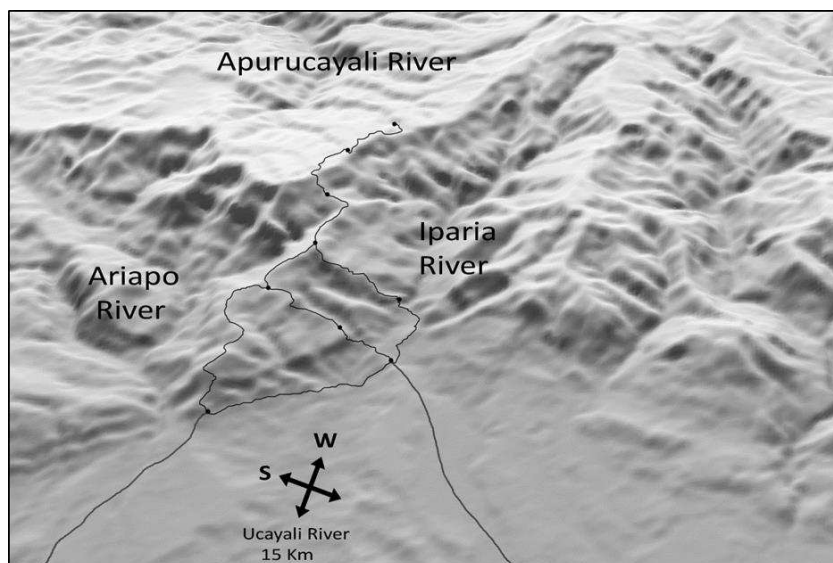


Figure 2. General landscape view of the study site, with trails and campsites illustrated.

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.

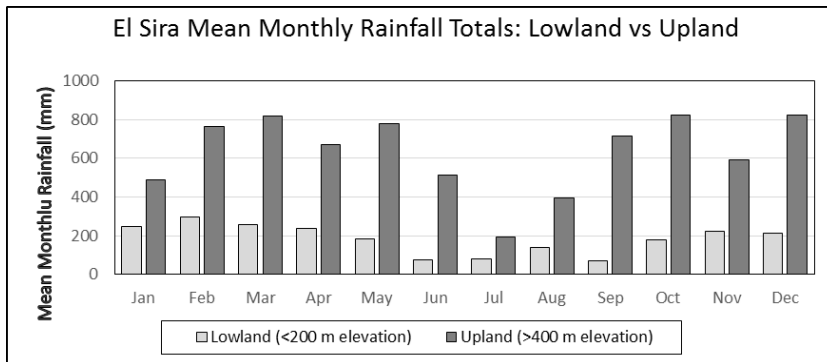


Figure 3. Mean monthly Rainfall (mm) comparing El Sira uplands vs. adjacent lowlands.

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.

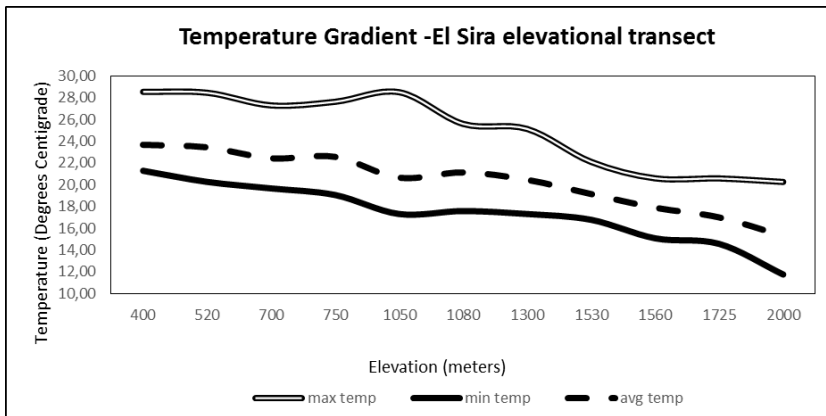


Figure 4. Temperature differentials measured along the slopes of our elevational transect in uplands of the El Sira Communal Reserve.

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.

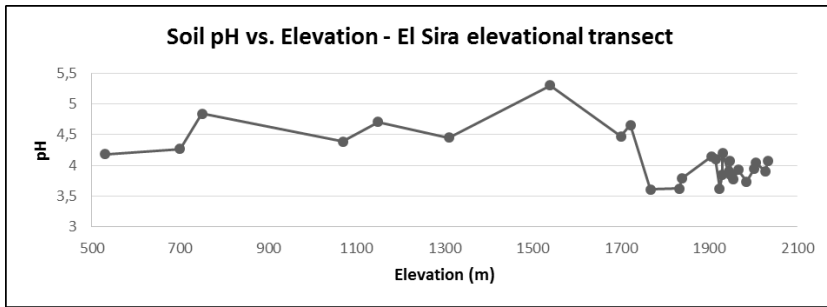


Figure 5. Soil pH as measured along our elevational transect in uplands of the El Sira Communal Reserve.

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							
Calypogeiaceae									
<i>Calypogeia lechleri</i> (Steph.) Steph.					1				
<i>Calypogeia peruviana</i> Nees & Mont.	1			2	2	4			
<i>Mnioloma caespitosum</i> (Spruce) R.M.Schust.				1					
<i>Mnioloma cellulosum</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) Vaña & 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>Cyclojeunea convexistipa</i> (Lehm. & Lindenb.) A. Evans				1	1x	x	x		
<i>Cyclojeunea peruviana</i> (Lehm. & Lindenb.) A. Evans					x	x	x		
<i>Diplasiojeunea brunnea</i> Steph.							x		x
<i>Diplasiojeunea cavifolia</i> Steph.		x			x	x			
<i>Diplasiojeunea caribea</i> Tixier									
<i>Diplasiojeunea inermis</i> Tixier					x	x	x	x	
<i>Diplasiojeunea johnsonii</i> A. Evans						x			
<i>Diplasiojeunea pauckertii</i> (Nees) Steph.			x						
<i>Diplasiojeunea pellucida</i> (Meissn.) Schiffn.							x	x	
<i>Diplasiojeunea</i> sp. nov.		1							
<i>Diplasiojeunea 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.

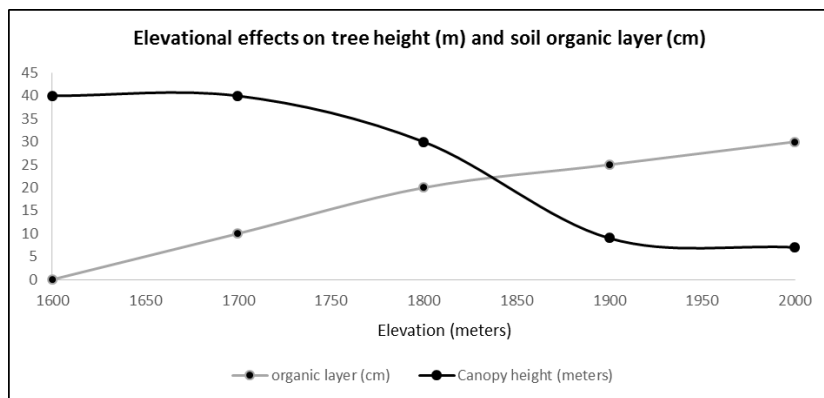


Figure 6. Elevational effects on mean tree canopy height (m) and soil organic layer (cm) between upper cloud forest and elfin forest formations on the steep slopes of the Ariapo uplift.

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:

**Anopolejeunea 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.

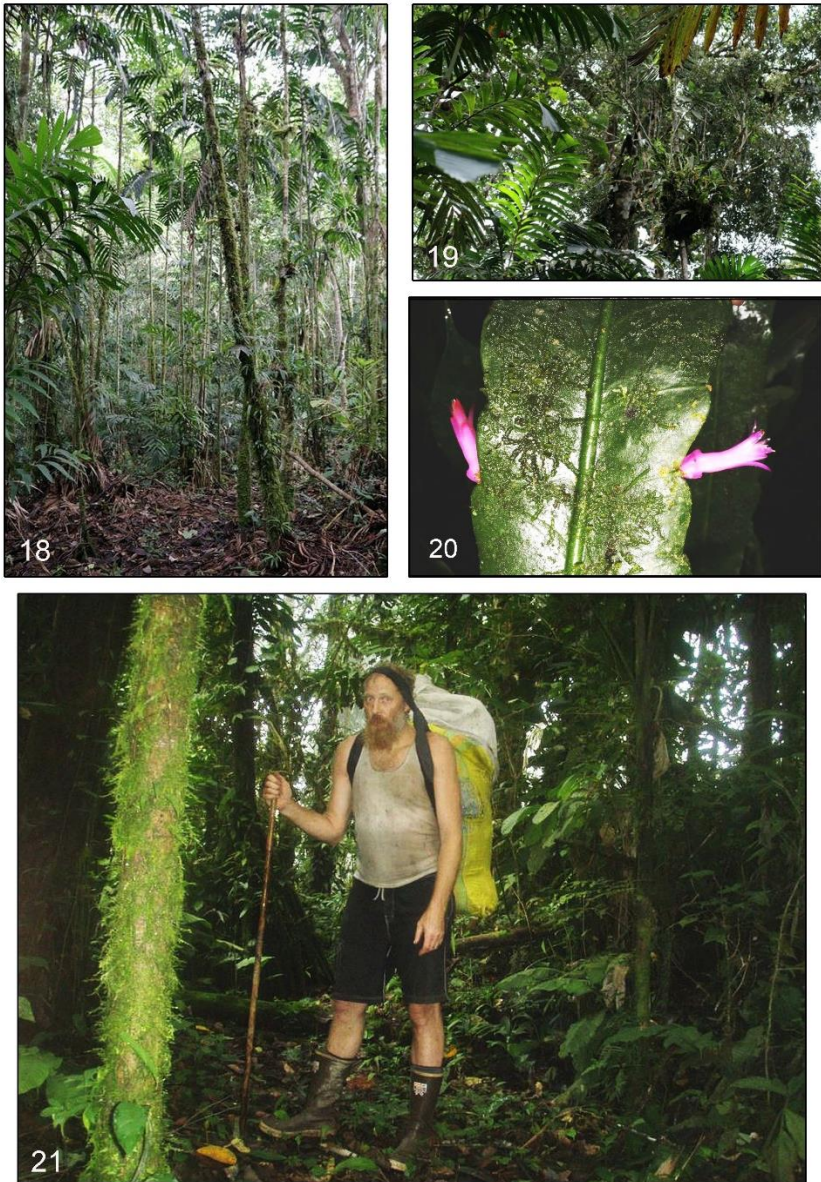


Plate IV. Photo 18. View of interior of lower cloud forest (3B) habitat, showing characteristic *Wettinia augusta* palm understory. **Photo 19.** View of canopy of lower cloud forest (3B) habitat. Woolly monkey visible in center of photo. **Photo 20.** View of epiphyllous liverworts on flowering cactus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

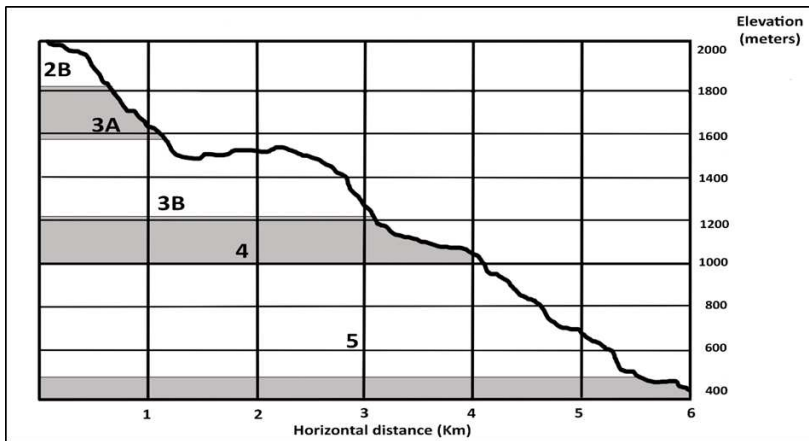


Figure 7. Elevational profile of transect and habitat types on the steep slopes of the Ariapo uplift. 2B. Elfin forest on sand. 3A. Upper cloud forest. 3B. lower cloud forest. 4. Transitional forest. 5. Premontane forest.

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.

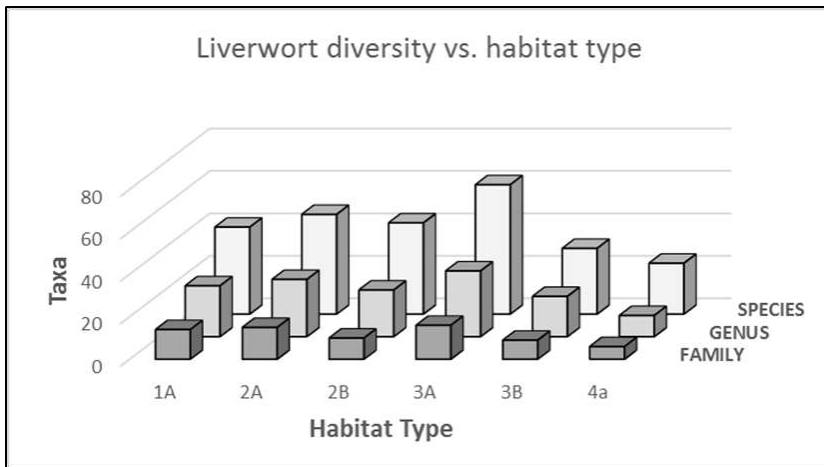


Figure 8. Relative diversity of non-epiphyllous liverwort collections by habitat type: Habitat 1A- 2000 meters elevation; 2A- 1900 m; 3A- 1850-2000 m; 3B- 1600-1850 m; Habitat 4- 1000-1250 m.

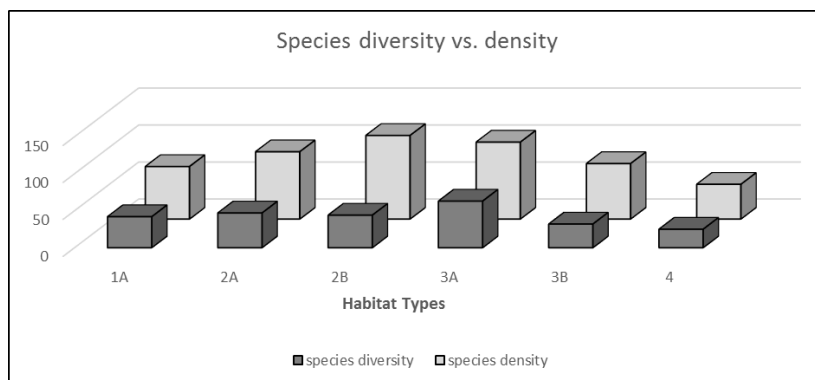
A clear pattern of liverwort diversity diminishing rapidly at lower elevations reveals itself in *Table 2*, which is typical of other Neotropical elevational inventories of bryophytes in Colombia, Peru, Guyana and French Guiana (Gradstein *et al.* 1995; Gehrig-Downie *et al.* 2013).

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	Prionolejaeunea aemula	Lejeuneaceae	Prionolejaeunea 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.

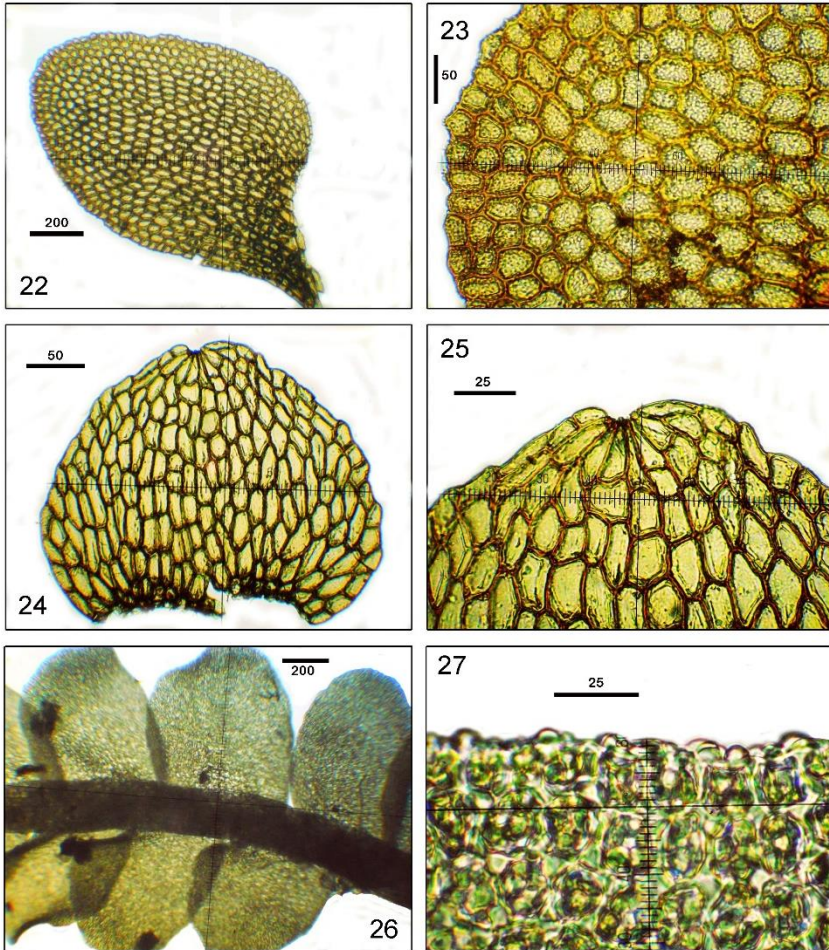


Plate V. Photos 22–25. *Mnioloma venezuelanum* (Fulford) R.M. Schust. from *Graham 6123*. 22: Leaf. 23: Leaf cells near margin. 24: Underleaf. 25: Underleaf apex cells. **Photos 26–27.** *Odontoschisma cleefii* Gradst., Aranda & Vanderp. from *Graham 6229*. 26: Habit, dorsal view. 27: leaf margin cells.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

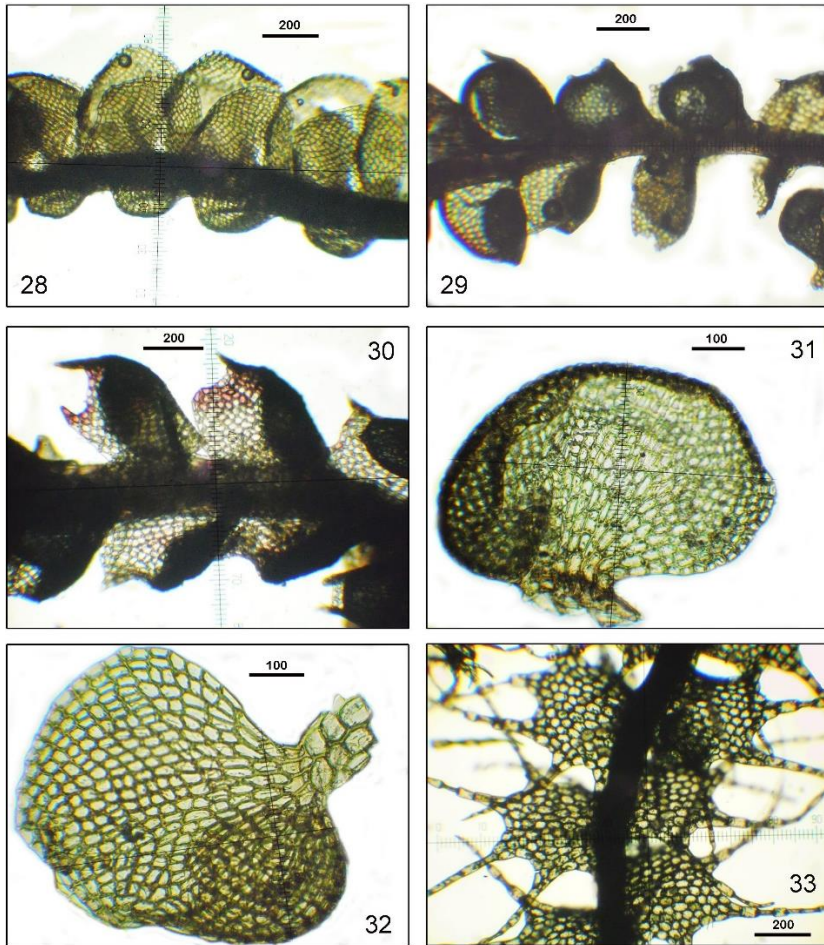


Plate VI. Photos 28–32. *Nowellia reedii* Robins. from *Graham 6594*. 28: Shoot with entire leaves. 29–30: Shoots with bilobed leaves. 30–31: Ventral and dorsal view of the seemingly entire leaves with a small lobe at their base. **Photo 33.** *Lophocolea orbigniana* Nees et Mont. from *Graham 7254*.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

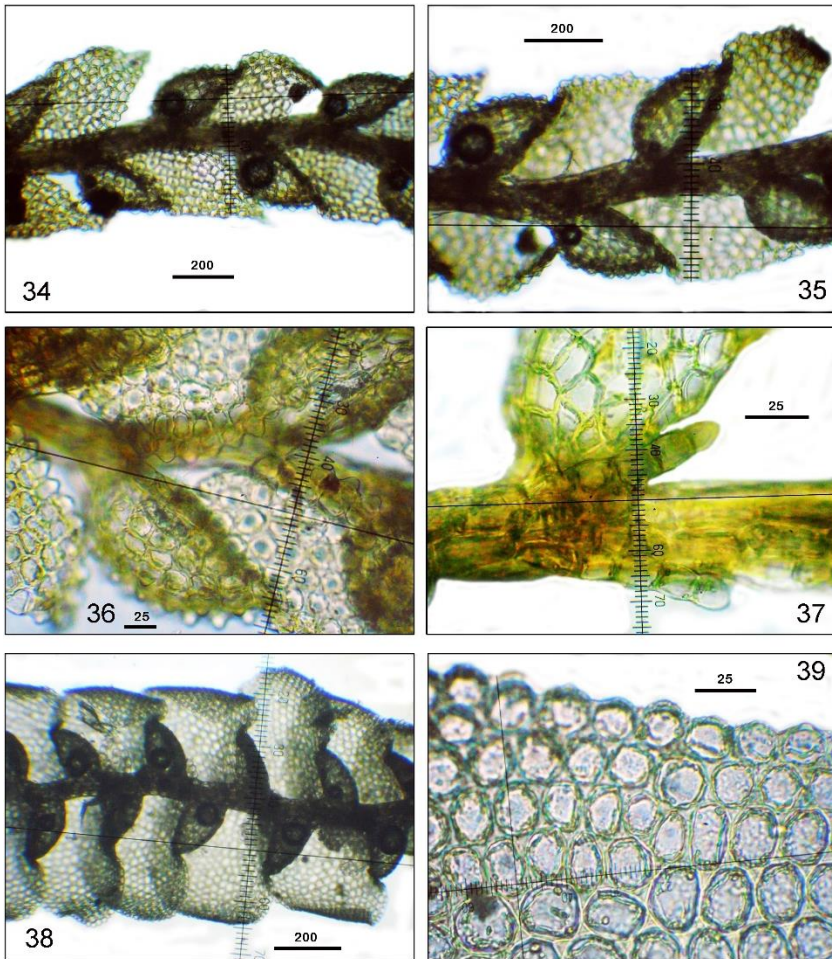


Plate VII. Photos 34–37. *Drepanolejeunea submuricata* R.M. Schust. from *Graham* 6347. 34 and 36: Shoot, dorsal views. 35 and 37: Shoot, ventral views. **Photos 38–39.** *Lejeunea* cf. *sporadica* Besch. & Spruce from *Graham* 6222. 38: Shoot, ventral view. 39: Leaf margin cells.

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).

Prionojeunea 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).

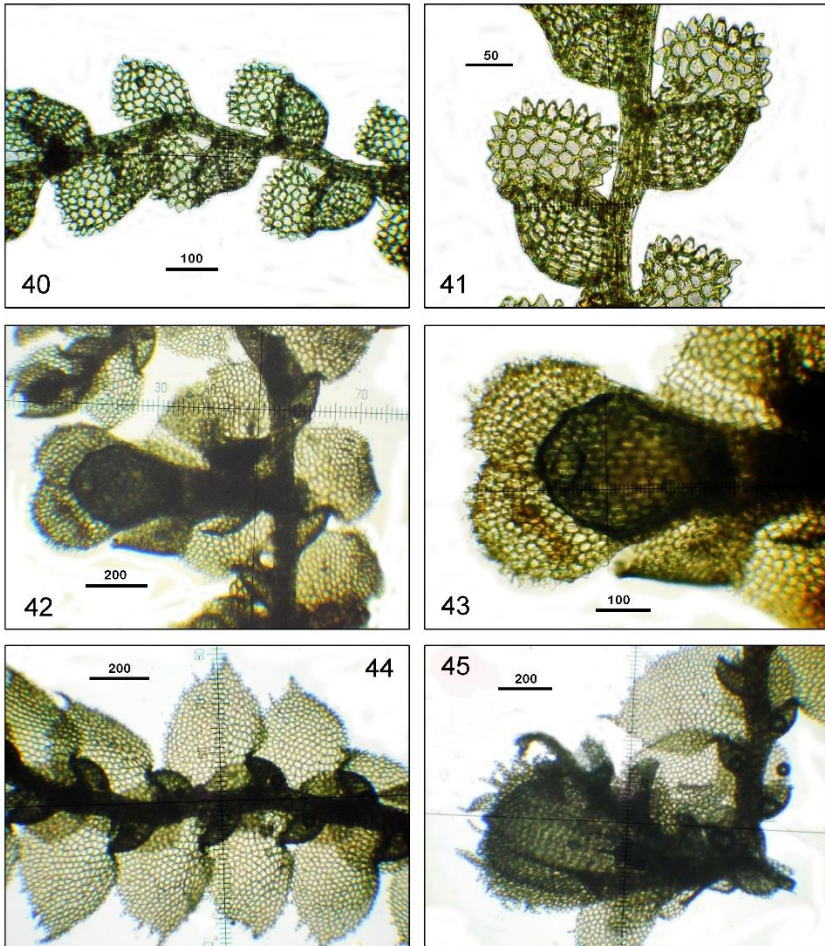


Plate VIII. Photos 40–41. *Lejeunea subspathulata* Spruce from Graham 6314. 40: Shoot, ventral view. 41: Shoot, dorsal view. **Photos 42–43.** *Prionolejeunea ampliretis* Herzog from Graham 6202. 42: Shoot, ventral view. 43: Perianth, ventral view. **Photos 44–45.** *Prionolejeunea decora* (Taylor) Steph.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

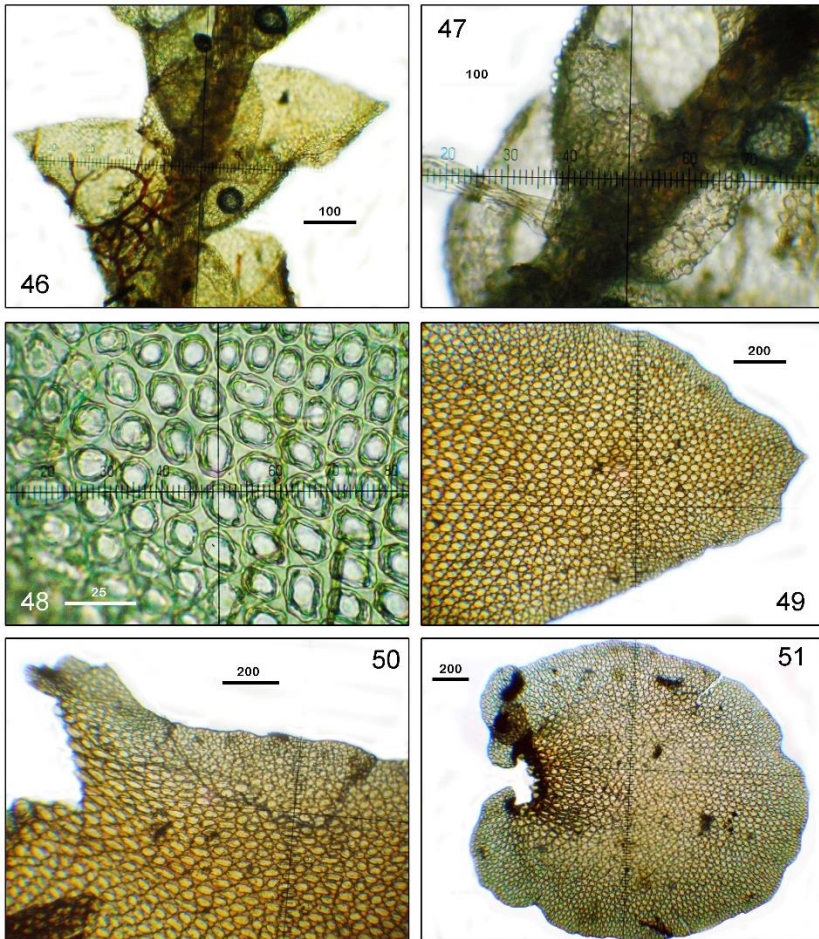


Plate IX. Photos 46–48. *Prionolejeunea trachyoides* (Spruce) Steph. from *Graham* 6388. 46: Shoot, ventral view. 47: Lobule with papillae, ventral view. 48: Median leaf cells with large papillae. **Photos 49–51.** *Bazzania canelensis* (Steph.) Fulford. from *Graham* 6623. 49: Leaf apex. 50: Postical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

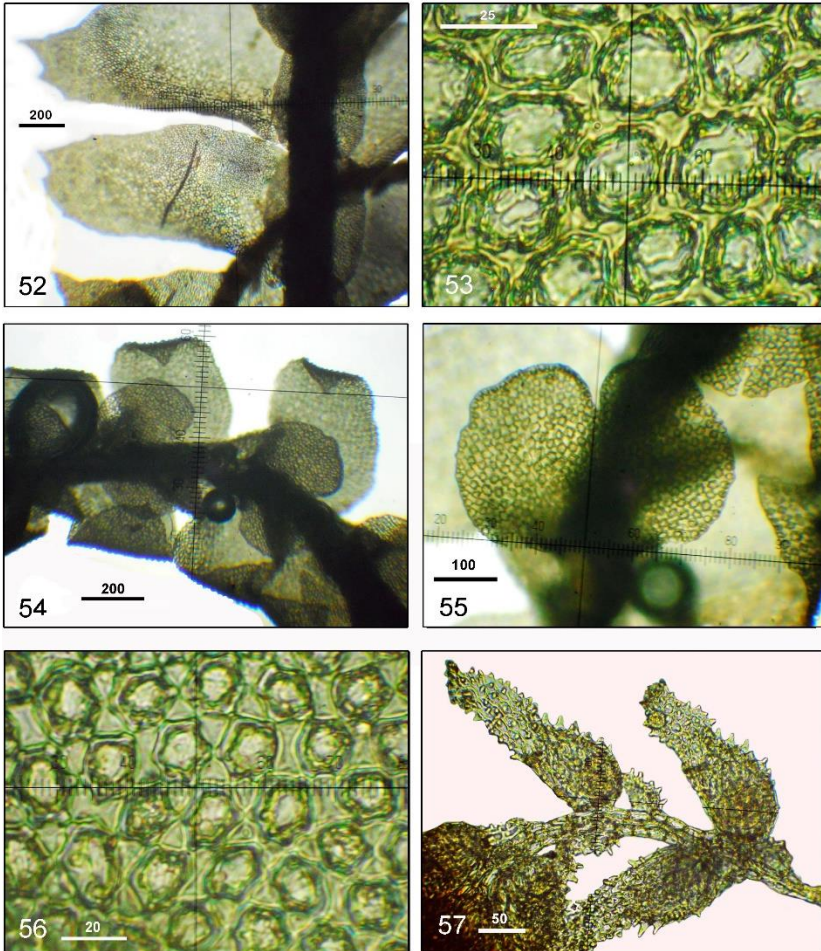


Plate X. Photos 52–53. *Bazzania cuneistipula* (Gottsche & Lindenb.) Trevis. from Graham 5496/B. 52: Shoot, ventral view. 53: Median leaf cells. **Photos 54–56.** *Cheilolejeunea* sp. aff. *Cheilolejeunea papillata* Solari from Graham 5407. 54: Habit, ventral view. 55: Underleaf. 56: Median lobe cells.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

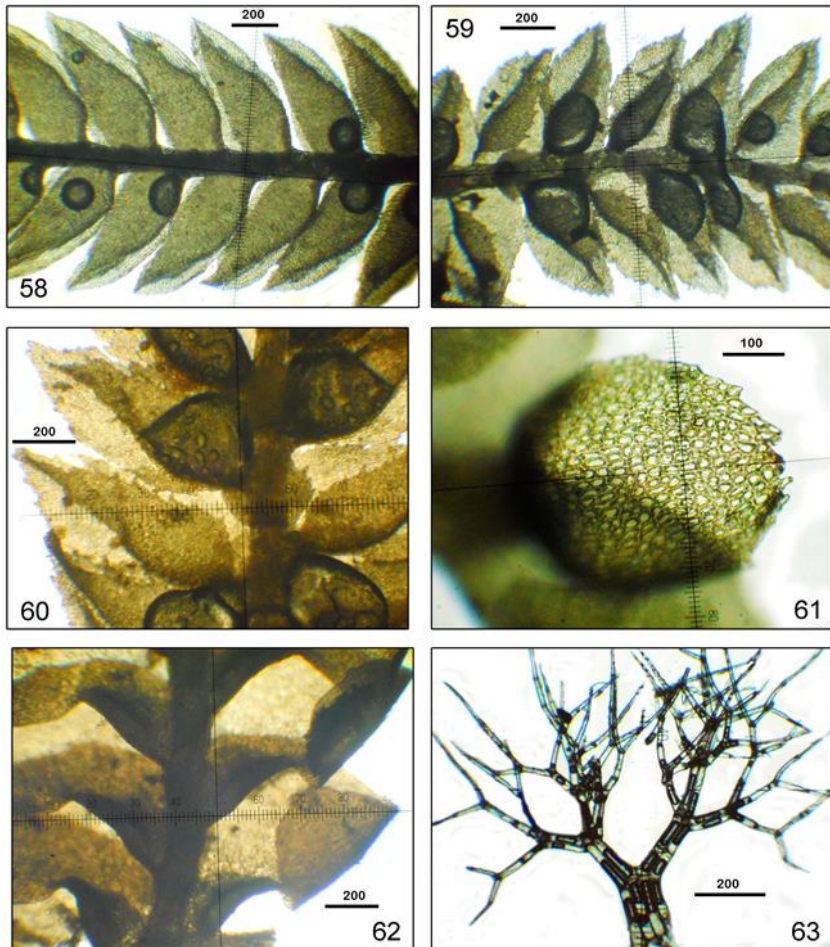


Plate XI. Photo 58. *Micropterygium parvistipulum* Spruce from *Graham 6204*, shoot ventral view. **Photo 59–61.** *Micropterygium reimersianum* Herzog from *Graham 6590*. 59 and 60: Shoot, ventral view. 61: Underleaf. **Photo 62.** *Radula involvens* Spruce from *Graham 6332*, shoot, ventral view. **Photo 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 ampliate, 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 pallidivirens, *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.

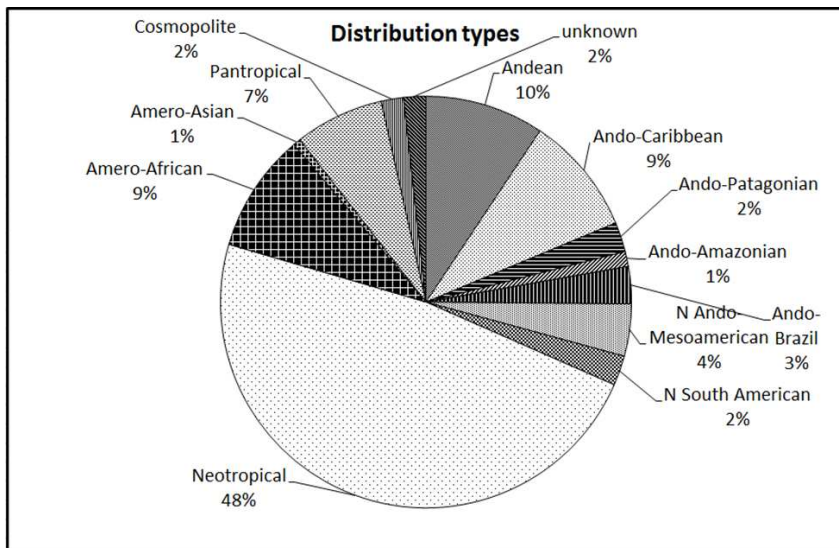


Figure 10. The ratio of the different distribution types in the investigated El Sira area.

Acknowledgements – We wish to thank the Jefatura of the El Sira Communal Reserve for their support of our research program over the years, and to extend our warmest regards to the native communities of the buffer zone of the Reserve adjacent to our study site, including Sharara, Puerto Nuevo, Dos de Mayo, Juancito de Sipiria, Amaquiria and Selva. Our sincere gratitude is extended to Carlos Reynel at Herbario Forestal, La Molina, Lima, Peru (MOL) for his enthusiastic support of our Peruvian research over the years. The support of colleagues Matt von Konrat and Anna Balla at the Field Museum (F), and Andrea Sass-Gyarmati at the herbarium of Eszterhazy Karoly University (EGR) is highly appreciated. T. Pócs acknowledges with thanks the opportunity to study this interesting liverwort material. Special thanks are due to Prof. S.R. Gradstein (PC) for his useful advice and corrections, also for supplying ample references and for placing at the disposal of the authors his unpublished book manuscript entitled the Guide to the liverworts of Columbia and Ecuador.

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.
- HEINRICH, J. (2002). A taxonomic revision of *Plagiochila* sect. *Hylacoetes*, sect. *Adiantoidae* and sect. *Fuscoluteae* in the Neotropics with a preliminary subdivision of Neotropical Plagiochilaceae into nine lineages. *Bryophyt. Biblioth.* **58**: 1–183.
- HEINRICH, 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.
- HEINRICH, 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.

(submitted: 30.11.2016, accepted: 08.12.2016)

SHORT-TERM CHANGES IN HEIGHT–DIAMETER RELATION OF TWO MAPLE SPECIES AND EUROPEAN CORNEL OF UNDERSTORY IN AN OAK FOREST IN HUNGARY ON THE BASIS OF TWO-PARAMETERS MODEL

Tamás Misik^{1*} & Károly Antal²

¹*Department of Environmental Science and Landscape Ecology, Eszterházy Károly University Eger, Hungary, 3300 Eger, Leányka u. 6;*

²*Department of Zoology, Eszterházy Károly University Eger, Hungary, 3300 Eger, Leányka u. 6; *E-mail: misiktom@gmail.com*

Abstract: Forest understory species such as shrub and herbaceous layer, have received little attention in long-term studies. Knowledge of the diameter and the height of trees are fundamental for developing growth and yield models in forest stands. Overstory composition of the Síkfőkút Project site was dominated by sessile oak–Turkey-oak forest (*Quercetum petraeae-cerris* Soó 1963). Similarly to other European countries an oak decline occurred in Hungary oak woodlands at the end of 1970's and about 63% of the oak trees perished in our site. The potential for oak species regeneration was a very low over the period of 1982-2012. Four nonlinear height-diameter functions were fitted and evaluated for Síkfőkút site based on a data set consisting of 2025 individuals for three dominant woody species (*Acer campestre* L., *Acer tataricum* L. and *Cornus mas* L.) and detected any short-term changes in these equations following dieback of oak canopies. These height-diameter equations increase our knowledge of the growth of these species; therefore will enable us to improve management planning in oak forests.

Keywords: oak decline, *Acer campestre*, shrub layer, size, growth model

INTRODUCTION

Knowledge of the diameter and the height of trees are fundamental for developing growth and yield models in forest stands (Lynch and Murphy 1995; Calama and Montero 2004). Many growth and yield systems use height and diameter as the two basic input variables, with all or part of the tree heights predicted from measured diameters (Arney 1985; Huang *et al.* 2000). The relation between the diameter of individuals and its height varies from one stand to another. Within the same forest stand, this relation is not constant

over time (Curtis 1967). Numerous generalized and region-wide equations have been developed recently for many tree species (e.g. Temesgen and Gadow 2004; Castedo Dorado *et al.* 2005). Equations for the height and the diameter relation of understory species are not typically in the international papers.

The height–diameter relationship has been calibrated following random-parameter models, using both repeated measurements from permanent plots (Lappi 1997) as well as cross-temporal measurements taken simultaneously in different temporary plots (Jayaraman and Lappi 2001). Linear mixed models were used by Mehtätalo (2004) for Norway spruce (*Picea abies* (L.) Karst.), Jayaraman and Zakrzewski (2001) for sugar maple (*Acer saccharum* Marsh.), and by Lynch *et al.* (2005) for cherrybark oak (*Quercus pagoda* Raf.). A number of height–diameter equations have been developed using only DBH of trees as the predictor variable for estimating total height (e.g. Larsen and Hann 1987; Fang and Bailey 1998; Peng 1999; Robinson and Wykoff 2004). Relation between the diameter of a tree and its height varies among stands (Calama and Montero 2004) and depends on the growing environment and stand conditions (Sharma and Zhang 2004). When actual height measurements are not available and difficult, height–diameter functions can also be used to indirectly predict height growth of individuals (Larsen and Hann 1987).

An increase in the death of oak forests has been observed in many regions of Hungary since 1978 (Igmándy 1987). The species composition of the canopy layer was stable until 1979 and the healthy *Q. petraea* and *Quercus cerris* L. (Turkey oak) also remained constant in the mixed-species forest stand (*Quercetum petraeae-cerris* Soó 1963) of Síkfőkút. Serious oak decline was first reported in 1979–80 and by 2012, 62.4% of the oaks had died; this decline resulted in an opening of the canopy and lead to changes in canopy and in understory dynamics.

The possible response of understory cover, basal area and diversity indices to stand density in our site has shown in the study of Misik *et al.* (2013). Diameter of a woody individuals can be measured quickly, easily, and accurately, but the measurement of height is relatively complex, time consuming, and difficult because of a big size of these individuals in our site. The dynamics increasing of height and diameter of woody species and the structure of new subcanopy layer were showed in the result of Misik *et al.* (2014).

The purposes of this study were (1) to fit and evaluate four height-diameter functions on a short-term data set covering *Acer campestre* L. (field maple), *Acer tataricum* L. (Tatar maple) and *Cornus mas* L. (European cornel) dominant woody species; (2) to identify the most appropriate height-diameter functions for three woody species, and (3) to detect some possible difference between these species on the basis of height-diameter functions during a 4-5 year periods.

MATERIALS AND METHODS

Study site

The 27 ha reserve research site is located in the Bükk Mountains of northeast Hungary (47°55' N, 20°46' E) at a distance of 6 km from the city of Eger at an altitude of 320–340 m a.s.l.. The site was established in 1972 by Jakucs (1985) for the long-term study of forest ecosystems. Mean annual temperature is 9.9 °C and mean annual precipitation ranges typically from 500 to 600 mm.

Description of the geographic, climatic, soil conditions and vegetation of the forest was undertaken in detail by Jakucs (1985, 1988). The most common forest association in this region is *Quercetum petraeae-cerris* with a dominant canopy of *Q. petraea* and *Q. cerris*. Both oak species are important dominant native deciduous tree species of the Hungarian natural woodlands. The plot under study is made up of evenly-aged trees, is at least 100 years old temperate deciduous forest and has not been harvested for more than 50 years.

Sampling and statistical analysis

Shoot analysis data of three dominant woody species (*A. campestre*, *A. tataricum* and *C. mas* are on the basis of the biggest mean size parameters in the shrub community) were obtained from a 27 ha study site at regular intervals. Monitoring activities started in 1982 and repeated shrub layer inventories took place in 1993, 1997, 2002, 2007 and 2012. The investigations were performed during the growing seasons.

Collected over the last 3 decades, the 2025 individuals were randomly selected throughout the study site to provide representative information for a variety of densities and heights of

dominant woody species. Summary statistics including the mean, minimum, maximum, and standard deviation (SD) for total shoot height and diameter of shoot by woody species are shown in *Table 1, 2 and 3.*

Table 1. *Acer campestre* shoot summary statistics based on dominant woody species.

Year	No. of sample specimens	Diameter (cm)				Total shoot height (m)			
		Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
1982	195	4.38	1.23	13.32	2.46	4.02	1.00	10.20	2.19
1993	151	6.70	1.40	18.00	3.55	5.17	1.30	15.00	3.05
1997	207	6.79	1.00	21.00	4.21	5.22	1.00	13.00	3.00
2002	160	8.49	0.82	35.00	6.54	6.06	1.10	17.00	3.54
2007	133	10.84	0.95	31.50	6.68	8.01	1.10	19.20	4.47
2012	125	10.63	0.85	37.92	6.02	7.60	1.18	16.50	3.76

Table 2. *Acer tataricum* shoot summary statistics based on dominant woody species.

Year	No. of sample specimens	Diameter (cm)				Total shoot height (m)			
		Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
1982	71	3.43	1.29	9.62	1.66	3.54	1.05	8.46	1.87
1993	45	4.69	1.30	10.10	2.35	3.37	1.30	7.00	1.54
1997	59	4.37	1.00	10.80	2.59	3.83	1.20	10.10	2.02
2002	45	5.28	0.42	14.19	3.68	4.32	1.20	8.10	2.28
2007	28	6.45	1.12	14.45	3.60	4.92	1.63	11.40	2.23
2012	24	7.40	0.59	14.41	3.94	5.50	1.70	8.95	2.29

Table 3. *Cornus mas* shoot summary statistics based on dominant woody species.

Year	No. of sample specimens	Diameter (cm)				Total shoot height (m)			
		Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
1982	155	3.93	1.28	8.92	1.64	3.52	1.05	13.00	1.74
1993	108	5.68	1.60	13.00	2.23	3.81	1.20	9.00	1.21
1997	193	4.97	1.10	13.40	2.58	3.97	1.00	9.60	1.82
2002	117	6.50	0.60	25.00	3.97	4.64	1.10	9.00	1.98
2007	116	7.36	0.80	29.63	5.39	4.63	1.10	8.40	2.04
2012	93	7.59	0.70	15.07	3.08	5.37	1.17	8.80	1.80

Four biparametric nonlinear equations were fitted and evaluated based on a data set consisting from a plot (*Table 4*). Radial and height growth are characterized for specimens of dominant woody species. Height and diameter of all living *Acer* spp. and *C. mas* in the high shrub layer (shrub individuals height ≥ 1.0 m were categorized as high shrubs) were measured with a scaled pole and at 5.0 cm above

the ground with a digital caliper and the measurement results were averaged.

Table 4. Nonlinear height-diameter functions selected for comparison.

Function No. and form*	References
[1] $H = 0.05 + e^{a+b / (D+1)}$	Wykoff <i>et al.</i> 1982
[2] $H = 0.05 + aD / (b + D)$	Bates and Watts 1980; Ratkowsky 1990
[3] $H = 0.05 + 10^a \times D^b$	Larson 1986
[4] $H = 0.05 + aD / (D + 1) + bD$	Watts 1983

* H = total tree height (m); D = diameter of shoot height (cm); a, b = parameters to be estimated; e = base of the natural logarithm (= 2.718 28); 0.05 is a constant used to account that diameter is measured at 0.05 m above the ground.

For each year of monitoring we fitted four nonlinear equations with two parameters (*Table 4*) describing the dependence of height on diameter. Height and diameter relationships of trees are generally described using nonlinear mathematical models. We replaced 1.3 with 0.05 m in the different height–diameter models, because we measured diameter of woody species in the understory at 0.05 m. When diameter approaches 0, H approaches 0.05 (e.g. if we use logistic type of function). The asymptotic *t*-statistics for the parameters and the plots of studentized residuals against the predicted height show that many concave and sigmoidal functions can be used to describe the height–diameter relationships. R Core Team (2014) and R package (Grothendieck 2013) were used to model the different nonlinear height-diameter functions. It was determined the most fitting nonlinear equations for each woody species on the basis of residual standard error values.

RESULTS

Tables 5, 6 and 7 show the least squares estimates of the parameters. Coefficient of determination (R^2) values ranged from 0.40 to 0.82, with the average being 0.70 of *A. campestre*, 0.59 of *A. tataricum* and 0.51 of *C. mas* during last three decades, and not reported here. Results in *Table 5, 6 and 7* show that for the two-parameter models, [2], [3] and [4] the *t*-statistics for the parameters of the functions are not significant at the 0.01 level of *A. campestre* and 0.05 level of the other two species in some studies.

Table 5. Parameter estimations for two-parameter height-diameter functions.

Function	Parameter	Estimates for <i>Acer campestre</i> in monitoring years					
		1982	1993	1997	2002	2007	2012
[1]	<i>a</i>	2.635	2.819	2.752	2.678	3.018	2.846
	<i>b</i>	-6.349	-8.691	-7.856	-6.763	-9.793	-8.346
[2]	<i>a</i>	44.650	90.350*	37.067	19.014	35.621	23.305
	<i>b</i>	43.770	111.070*	39.855	15.115	34.661	19.767
[3]	<i>a</i>	0.040*	-0.043*	0.041*	0.257	0.166	0.260
	<i>b</i>	0.882	0.913	0.824	0.600	0.728	0.623
[4]	<i>a</i>	0.763	0.702*	1.219	3.498	2.627	3.600
	<i>b</i>	0.772	0.675	0.615	0.376	0.524	0.416

Note: *The asymptotic *t*-statistic for the parameter is not significant at the 0.01 level.

The residual standard errors (RSE) of three woody species are summarized in Table 8. The most fitted height-diameter function values for woody species showed in bold. Function of Wykoff *et al.* (1982) generally giving the most suitable results, except of *A. campestre*.

Table 6. Parameter estimations for two-parameter height-diameter functions.

Function	Parameter	Estimates for <i>Acer tataricum</i> in monitoring years					
		1982	1993	1997	2002	2007	2012
[1]	<i>a</i>	2.639	1.986	2.239	2.302	2.280	2.355
	<i>b</i>	-5.959	-4.057	-4.355	-4.420	-4.436	-4.814
[2]	<i>a</i>	47.180*	8.969	12.775	12.139	11.500	11.971
	<i>b</i>	42.120*	7.287	9.430	8.048	7.553	7.714*
[3]	<i>a</i>	0.056*	0.129*	0.173	0.227	0.257	0.309
	<i>b</i>	0.917	0.604	0.658	0.601	0.557	0.514
[4]	<i>a</i>	0.462*	2.040	2.096	2.688	3.113	3.700
	<i>b</i>	0.916	0.364	0.498	0.427	0.365	0.320

Note: *The asymptotic *t*-statistic for the parameter is not significant at the 0.05 level.

Table 7. Parameter estimations for two-parameter height-diameter functions.

Function	Parameter	Estimates for <i>Cornus mas</i> in monitoring years					
		1982	1993	1997	2002	2007	2012
[1]	<i>a</i>	2.361	1.983	2.225	2.158	2.113	2.181
	<i>b</i>	-5.268	-4.070	-4.623	-3.978	-3.745	-3.863
[2]	<i>a</i>	24.380	8.504	13.204	9.290	8.707	9.926
	<i>b</i>	23.110*	6.666	10.870	5.478	4.889	5.858
[3]	<i>a</i>	0.040*	0.167	0.130	0.322	0.332	0.301
	<i>b</i>	0.850	0.554	0.684	0.448	0.417	0.497
[4]	<i>a</i>	0.813*	2.415	1.842	4.181	4.296	3.524
	<i>b</i>	0.723	0.310	0.495	0.190	0.157	0.306

Note: *The asymptotic *t*-statistic for the parameter is not significant at the 0.05 level.

Function of Watts (1983) has very poor convenience and large RSE values; this function was fitted for *A. campestre* only in two different times. The lower error values were measured in 1982 and in 1993,

later these values increased in line with increasing average size of dominant woody species.

Table 8. Comparison of nonlinear height-diameter function: residual standard errors.

Function	Species	Residual standard errors					
		1982	1993	1997	2002	2007	2012
[1]	<i>Acer campestre</i>	1.021	1.965	1.347	1.684	2.496	2.189
	<i>Acer tataricum</i>	1.029	1.134	1.362	1.003	1.359	1.510
	<i>Cornus mas</i>	1.205	0.828	1.091	1.245	1.104	1.251
[2]	<i>Acer campestre</i>	0.972	1.869	1.262	1.678	2.404	2.207
	<i>Acer tataricum</i>	1.028*	1.131	1.348	1.008	1.360	1.513
	<i>Cornus mas</i>	1.202*	0.827	1.079	1.256	1.117	1.247
[3]	<i>Acer campestre</i>	0.972	1.866	1.267	1.784	2.423	2.318
	<i>Acer tataricum</i>	1.033	1.133	1.347	1.055	1.405	1.546
	<i>Cornus mas</i>	1.204*	0.836	1.078	1.354	1.249	1.256
[4]	<i>Acer campestre</i>	0.973	1.862	1.277	1.906	2.461	2.437
	<i>Acer tataricum</i>	1.036	1.137	1.351	1.096	1.438	1.576
	<i>Cornus mas</i>	1.205*	0.844	1.082	1.399	1.286	1.265

Note: The most fitted height-diameter function values shown in bold.

*The RSE values are not compared because of insignificant *t*-statistics.

The most fitted function for *Acer* species and *C. mas* are shown in Figure 1, 2 and 3. Standard error values for the fitted functions, although not reported here, ranged from 0.03 to 116.21, with the average being 7.76 of *A. campestre*, 3.00 of *A. tataricum* and finally 1.16 of *C. mas* during monitoring investigations.

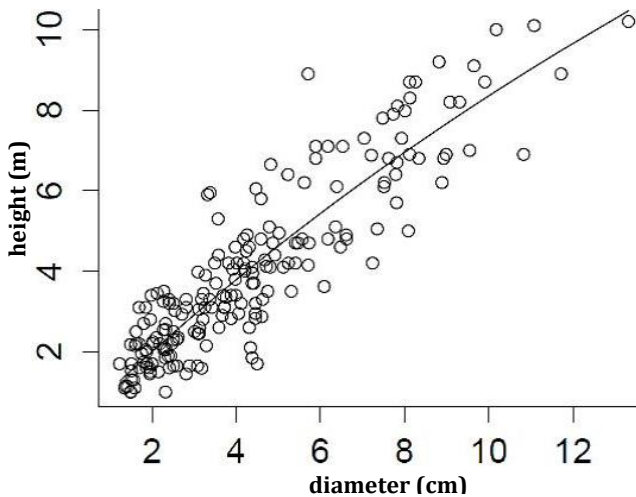


Figure 1. Plot of total tree height against diameter for *Acer campestre* in 1982. The curve was produced by [2] function.

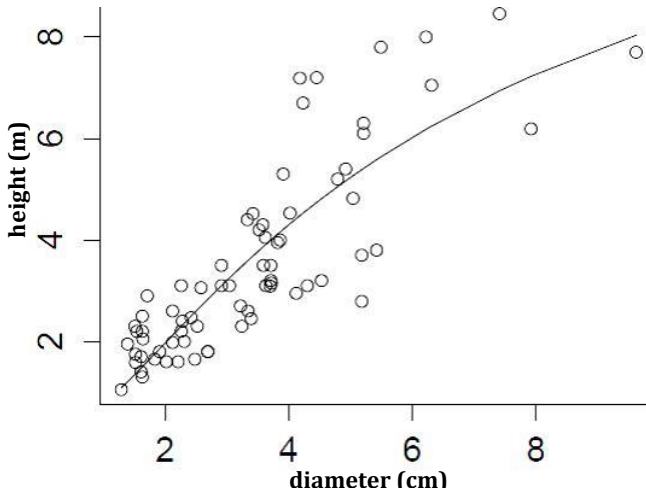


Figure 2. Plot of total tree height against diameter for *Acer tataricum* in 2002. The curve was produced by [1] function.

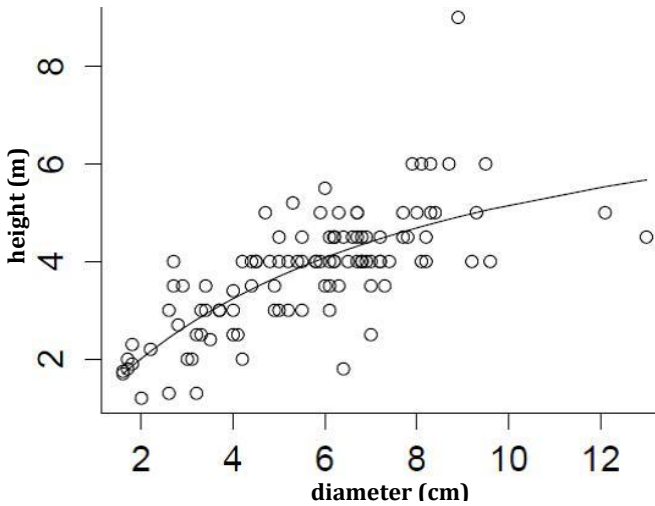


Figure 3. Plot of total tree height against diameter for *Cornus mas* in 1993. The curve was produced by [2] function.

DISCUSSION

The aim of this study was to develop a model capable of predicting the oak death pattern in Síkfökút oak forest for height-diameter relation of dominant woody species and basic calculation of forest inventories. Woody shoot height is an important variable which is used for estimating stand volume, site quality and for describing understory structure following serious oak decline.

It's known that due to competition, trees with the same diameter are taller in denser forest stands. Density and diameter are not only necessary, but may be sufficient for determining tree height because other factors affecting height are reflected by diameter and density. In the process of developing the proposed model it was found that height increases monotonically with density and that this increase is not bounded by an asymptote (Zeide and Vanderschaaf 2002). Our study is in agreement with this statement of previous finding because *A. campestre* increased in density (from 56 to 204 specimen's ha⁻¹); density of *A. tataricum* and *C. mas* did not changed in importance in the subcanopy layer over the past 3 decades (Misik *et al.* 2014).

Kenefic and Nyland (1999) explored sugar maple height diameter and age diameter relationship in a balanced uneven-aged northern hardwood in USA. They results suggest that regressions show a clear relationship between tree diameter and height in the studied stand. When interpreted in light of the correlation between tree diameter and age, these results suggest a relationship between tree age and height as well. The height parameters vary considerably with diameter; this relationship can be described by statistically valid equation.

Conclusions to be derived from the site are as follows: (1) it was fitted and evaluated four height-diameter functions on a long-term data set covering dominant woody species. (2) The most appropriate height-diameter functions were Wykoff *et al.* (1982) for *A. tataricum* and *C. mas* and Bates and Watts (1980) and Ratkowsky (1990) for *A. campestre*. (3) After the oak decline in the study site was detected remarkably increasing of residual standard errors for these species. This increasing was the lowest by *C. mas* species. These fitted and evaluated equations increase our knowledge of the growth of this species and therefore will enable us to improve management planning in oak forests.

REFERENCES

- ARNEY, J.D. (1985). A modeling strategy for the growth projection of managed stands. *Canadian Journal of Forest Research* **15**: 511–518.
- CALAMA, R. & MONTERO, G. (2004). Interregional nonlinear height–diameter model with random coefficients for stone pine in Spain. *Canadian Journal of Forest Research* **34**: 150–163.
- CASTEDO DORADO, F., BARRIO ANTA, M., PARRESOL, B.R., & ÁLVAREZ GONZÁLEZ, J.G. (2005). A stochastic height–diameter model for maritime pine ecoregions in Galicia (northwestern Spain). *Annals of Forest Science* **62**: 455–465.
- CURTIS, R.O. (1967). Height–diameter and height–diameter–age equations for second-growth Douglas-fir. *Forest Science* **13**: 365–375.
- FANG, Z. & BAILEY, R.L. (1998). Height–diameter models for tropical forests on Hainan Island in southern China. *Forest Ecology and Management* **110**: 315–327.
- GROTHENDIECK, G. (2013). Non-linear regression with brute force. R package version 0.2.
- HUANG, S., PRICE, D., & TITUS, S.J. (2000). Development of ecoregion-based height–diameter models for white spruce in boreal forests. *Forest Ecology and Management* **129**: 125–141.
- IGMÁNDY, Z. (1987). Die Welkeepidemie von *Quercus petraea* (Matt.) Lieb. in Ungarn (1978 bis 1986). *Österreichische Forstzeitung* **98**: 48–50.
- JAKUCS, P. (ed., 1985). *Ecology of an oak forest in Hungary*. Akadémia Kiadó, Budapest, 545 pp.
- JAKUCS, P. (1988). Ecological approach to forest decline in Hungary. *Ambio* **17**: 267–274.
- JAYARAMAN, K. & LAPPI, J. (2001). Estimation of height–diameter curves through multilevel models with special reference to even-aged teak stands. *Forest Ecology and Management* **142**: 155–162.
- JAYARAMAN, K. & ZAKRZEWSKI, W.T. (2001). Practical approaches to calibrating height–diameter relationships for natural maple stand in Ontario. *Forest Ecology and Management* **148**: 169–177.
- KENEFIC, L.S. & NYLAND, R.D. (1999). Sugar maple height–diameter and age–diameter relationships in an uneven-aged northern hardwood stand. *Northern Journal of Applied Forestry* **16**: 43–47.
- LAPPI, J. (1997). A longitudinal analysis of height/diameter curves. *Forest Science* **43**: 555–570.
- LARSEN, D.R. & HANN, D.W. (1987). *Height–diameter equations for seventeen tree species in southwest Oregon*. Oregon State University, Forest Research Laboratory, Corvallis, Research Paper 49. pp.
- LYNCH, T. & MURPHY, P. (1995). A compatible height prediction and projection system for individual trees in natural, even-aged shortleaf pine stands. *Forest Science* **41**: 194–209.
- LYNCH, T.B., HOLLEY, A.G., & STEVENSON, D.J. (2005). A random-parameter height–dbh model for cherrybark oak. *Southern Journal of Applied Forestry* **29**: 22–26.
- MEHTÄTALO, L. (2004). A longitudinal height–diameter model for Norway spruce in Finland. *Canadian Journal of Forest Research* **34**: 131–140.

- MISIK, T., VARGA, K., VERES, ZS., KÁRÁSZ, I., & TÓTHMÉRÉSZ, B. (2013). Long-term response of understorey cover, basal area and diversity to stand density in a mixed oak forest on the Síkfőkút plot in Hungary. *Journal of Forest Science* **59**: 319–327.
- MISIK, T., KÁRÁSZ, I., & TÓTHMÉRÉSZ, B. (2014). Understorey development in an oak forest in northern-Hungary: the subcanopy layer. *Acta Silvatica et Lignaria Hungarica* **10**: 9–21.
- PENG, C.H. (1999). *Nonlinear height–diameter models for nine tree species in Ontario boreal forests*. Ontario Forest Research Institute, Ministry of Natural Resources, Sault Ste Marie, Ontario, Forest research report No. 155. pp. 28.
- R CORE TEAM (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- ROBINSON, A.P. & WYKOFF, W.R. (2004). Imputing missing height measures using a mixed-effects modeling strategy. *Canadian Journal of Forest Research* **34**: 2492–2500.
- SHARMA, M. & ZHANG, S.Y. (2004). Height–diameter models using stand characteristics for *Pinus banksiana* and *Picea mariana*. *Scandinavian Journal of Forest Research* **19**: 442–451.
- TEMESGEN, H. & GADOW, K.V. (2004). Generalized height-diameter models an application for major tree species in complex stands of interior British Columbia. *European Journal of Forest Research* **123**: 45–51.
- ZEIDE, B. & VANDERSCHAAF, C. (2002). The effect of density on the height-diameter relationship. In: Gen. Tech. Rep. SRS-48. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. pp. 463–466.

(submitted: 29.10.2015, accepted: 16.07.2016)

REDISCOVERY OF *CAMPANULA MACROSTACHYA* WALDST. & KIT. EX WILLD. IN THE BÜKK FOOTHILLS

András Schmotzer¹* & Jana Táborská²

¹Bükk National Park Directorate, Sánc u. 6, H-3304 Eger, Hungary;

²Department of Botany and Plant Physiology, Eszterházy Károly University, Leányka u. 6, H-3300 Eger, Hungary; *E-mail: schmotzera@bnpi.hu

Abstract: The single recent stand of the strictly protected *Campanula macrostachya* Waldst. & Kit. ex Willd. from the Bükk Mts. is presented in this paper. This Pontic-Pannonian-Balkan element is rather scattered in the western and northern parts of its range and has been regarded in past decades as an “extinct” or “non-confirmed” species in the Bükk Mountains. The occurrence of this species in this region was first documented as far back as 1910 by Gyula Prodán. The second and last occurrence was documented with a herbarium specimen by Rezső Soó in 1938. No proved occurrence had been known in the last seven decades from the region, until when in 2015 a new locality was found among orchards in a secondary steppe grassland in the Bükk foothills, close to the village of Szomolya. This contribution also includes a description of the habitat based on three phytosociological relevés, a photocopy of the voucher specimen and a line drawing of the species.

Keywords: *Campanulaceae*, distribution, rediscovery, Bükk Mts., habitat preference

INTRODUCTION

Campanula macrostachya Waldst. & Kit. ex Willd. (syn.: *C. macrostachya* Willd.; *C. multiflora* Waldst. & Kit.; *C. cervicaria* subsp. *macrostachya* (Waldst. & Kit. ex Willd.) Tacik) is a lowland-colline, Pontic-Pannonian-Balkan flora element (Fedorov 1957, Soó 1968, Fedorov and Kovanda 1976). According to current knowledge, it is distributed from the Ukrainian steppe zone through Anatolia and the Balkan Peninsula to the Carpathian Basin (Meusel and Jäger 1992). The occurrence of the species in the Balkans is restricted to the eastern and central parts, including Serbia, Montenegro, Macedonia, Bulgaria, Greece (Thrace) and the European part of Turkey (Obradović 1974, Damboldt 1978, Kovačić 2004, Teofilovski 2011, Kožuharov and Anchev 2012). It was recently clarified that the

species was erroneously reported from Albania (Barina *et al.* 2016). A taxon described as *C. macedonica* by Boissier (1875) is treated now as the synonym of *C. macrostachya* (EURO+MED 2006). The species is also present in Eastern Europe, with sporadic data known from the eastern parts of Romania and Moldavia (Oprea 2005, Ciocârlan 2009, Shabanova *et al.* 2014). As many other steppe and forest-steppe plants, this species also reaches its western and northern distribution limit in the Carpathian Basin (Sag and Gotthard 1985, Holub 1999, Fekete *et al.* 2011). In the Carpathian Basin, it occurs in Romania (Transylvania), southern Slovakia and northern Hungary (Oprea 2005, Marhold and Hindák 1998, Goliašová *et al.* 2008, Király 2009). The Slovak and Hungarian populations are partly distributed in the same phytographical region (“Matricum”). Its native range is rather disjunct, showing regression especially at the western and northern borders of its range.

Campanula macrostachya is also a rare, scattered plant in Hungary. It occurs on warm, southern-faced slopes in hilly areas from the Balaton Uplands to the Bükk Mountains and on one volcanic hill on the Bereg Plain (Király 2009). In most of the regions *C. macrostachya* has only been reported from few (usually less than 3) locations (e.g. Börzsöny Mts. /Nagy 2007/, Cserhát /Malatinszky *et al.* 2014/, Bereg Plain /Fintha 1994/). The occurrence of the species in the Gerecse Mountains has recently proved unconfirmed and the data in question are now considered to be an error (Barina 2006). The most viable populations of the species occur around Budapest (esp. Visegrád Mts and Pilis; Bóhm 2001, Barina 2004) and in the Mátra Mts (Soó 1937, Sramkó *et al.* 2008). Further localities of the species were mapped during the last decade in the Mátra Mts. (Magos G. *pers. comm.*). The species' recent distribution is indicated from 13 grid quadrates in the flora atlas of Hungary (Bartha *et al.* 2015).

Campanula macrostachya is a strictly protected plant species in Hungary and in Slovakia. Due to its rarity and phytogeographic importance, the species is also included in national and regional red lists. According to the Hungarian and the Slovakian red lists the species is evaluated as “endangered” (EN) (Király 2007, Eliáš *et al.* 2015). The species was also included in regional red lists, especially in a Carpathian regional context. In the Carpathians, it was categorised as “vulnerable” (VU) (Witkowski *et al.* 2003) or recently as “near threatened” (NT) (Turis *et al.* 2014a). The species was also

evaluated as “endangered” in the Carpathian part of Slovakia (Turis *et al.* 2014b).

The objectives of this study are (i) to present the current occurrence of the species in the Bükk Mts. and (ii) to characterise its newly discovered locality and remark on its future prospects.

MATERIALS AND METHODS

The study species

As many other Pannonian plant species, *C. macrostachya* was discovered by Jacob Winterl, who named it *Campanula petraea* (Winterl 1788). His descriptions and nomenclatures were not valid, so the valid description was published, inter alia, by Willdenow (1809), based on the collection of Waldstein and Kitaibel (Kováts 1992, Barina 2014). They described and presented the species as *Campanula multiflora* in the third volume of their master work, “Descriptiones et Icones Plantarum Rariorum Hungariae” (Waldstein and Kitaibel 1811).

Campanula macrostachya belongs to the *Involucratae* (Fomin) Charadze subsection of the *Campanulaceae* family. This subsection is characterized by sessile flowers that are crowded in heads, whorls or clusters and flowers are enveloped by large bracts, which facilitate secondary diaspore presentation (Fedorov 1957). Species of this subsection are usually more or less densely pubescent. The closest relatives of this species in the Pannonian flora district are *Campanula glomerata* L. and *C. cervicaria* L. It is a typical short lived perennial herbaceous species, which means that the plant grows longer than one year vegetatively before completing its life cycle after the first and only generative reproduction. Despite that, some authors treat *C. macrostachya* as a biennial plant (e.g. Damboldt 1978, Ciocârlan 2009).

The plants are up to 70 cm tall, the stem is erect, simple, striate and leafy. The basal leaves are crenate or entire, withered at anthesis; cauline lanceolate, sessile, the uppermost ovate-lanceolate, cordate. Flowers are in clusters of 3–5. The inflorescences are branched, interrupted-spicate. The calyx-teeth are lanceolate, $\frac{1}{3}$ as long as the corolla. The corolla is narrowly infundibular, 10–15(–20) mm long, usually pale-violet blue. The capsule is obconical, constricted at apex, 4–5 × 2–3 mm and opening by 3 small capsules (Fedorov & Kovanda 1976, Király 2009; *Figure 1*). Actual

karyological data on tetraploid populations occurring in Hungary (2n=32; locality: Visegrád Mts.) were reported by Michalková (2007).



Figure 1. *Campanula macrostachya* Waldst. & Kit. ex Willd. (drawn by J. Tábořská).

The study area

The Bükk Mountains belong to the inner range of the Carpathians (as part of the Western Carpathians, see Kondracki 1978) and are different from the neighbouring mountains both in origin and structure. The area is very diverse petrographically, includes a massive part of cavernous limestone on the Bükk Plateau (Sütő *et al.* 2015), complemented by other non-karstic rocks (such as porphyry, slate shale and basalt). The Bükk foothills (“Bükkalja”) as a separate landscape are petrographically varied, the young surface was formed by volcanites (ignimbrite, rhyolite, rhyolite tuff), covered with Pliocene and Pleistocene deposits (e.g. sand, marl and loess; Balogh 1964, Pelikán 2005). The whole area of the Bükk Mts belongs to the Borsodense flora-district of the Matricum flora-region of the Pannonian flora province. It is the largest area with the most varied flora and vegetation not only of the Hungarian Northern Mountain Range but of the whole of Hungary. Floristically it is even more interesting that dealpine-glacial and sub-Mediterranean-interglacial and, moreover, cold-continental species can be found here, and endemic and sub-endemic plants are also notable (Vojtkó 2001). The presence of steppe and forest steppe species are also remarkable, especially on the Bükk foothills and in the southern Bükk Mts (Schmotzer 2015).

Data acquisition and processing

The field work was carried out during the years 2015 and 2016. Concentrating on the occurrences of *C. macrostachya* in the Bükk Mts. and its surroundings, the relevant herbarium collections were studied. The primary data were obtained from specimens in herbarium collections, but only one specimen of the species was found from the Bükk Mts. in the collection of the Herbarium Carpato-Pannonicum Budapest (BP). The vascular collection of Eszterházy Károly University (EGR) was also checked. The online herbarium database of Debrecen University collections (DE) (Takács *et al.* 2015a, b) was also investigated. All literature data were evaluated in this study, including non-reliable secondary data, published in regional and national publications. As for related papers, we tried to detect the original data sources. Data without precise coordinates were indicated (e.g. old records without any lower toponyms). In such a case the more suitable location for the species was chosen in the process of the GIS interpretation. The CEU grid numbers added

follow the codes of the Central European Flora-mapping project (Niklfeld 1971, Király 2003). The distribution map was produced using ArcGIS 10.3 software. Geo-coordinates of the localities were determined using a Trimble Juno 3B GPS device in Hungarian EOVI DATUM projection. The coordinates were converted to the WGS-84 system by the online application of Psoft Informatikai Ltd. (www.psoft.hu). Online historical maps of the Habsburg Empire and cadastral maps were used to study former land-use of the study area (<http://mapire.eu/en/>).

For describing the habitat conditions of the discovered new locality, we carried out three phytosociological relevés, according to the Central-European Phytosociological School method (Braun-Blanquet 1932). We sampled vegetation patches where *Campanula macrostachya* covers at least 0.5% of the relevé size. We presented percentage cover data for the vascular plant species. Coverage below 0.5% is indicated as “+” and the mark “a” is used to refer for accidental elements. Nomenclature of flowering plants is according to Király (2009). Nomenclature of plant syntaxa follows Borhidi *et al.* (2012).

The voucher specimen was deposited in the Herbarium Carpato-Pannonicum collection of the Hungarian Natural History Museum, Budapest (ID number: BP7510721; *Figure 2*).

RESULTS AND DISCUSSION

Discovery of the new locality of *Campanula macrostachya* in the Bükk foothills

On 21 April 2015, the first author carried out spring-time floristic mapping in the Bükk foothills to gather additional protected or vulnerable plant species within the framework of an intensive floramapping of the region (see Schmotzer 2015). While collecting GPS data of e.g. *Orchis morio*, *Thlaspi jankae*, *Prunus tenella*, *Vinca herbacea*, he found some basal leaves which resembled *Campanula macrostachya*. The verification of this identification was made on 7 July 2015, when the plants were in late flowering state. We revisited the site on 16 June 2016, estimated the population size, expanded the flora-list of the locality and carried out the phytosociological relevés.



Figure 2. Voucher specimen of *Campanula macrostachya* (ID number: BP7510721) (photo by Cs. Németh).

The locality is situated on Gyűr Hill (in Hungarian: “Gyűr-tető”; part “Csáj-szél”), approx. 300 metres east of Szomolya village (Borsod-Abaúj-Zemplén county, North-Hungary; CEU mapping unit: 8189/1). The average height of the locality is 230–235 metres a.s.l. Centroid coordinates of the locality are 47.8896° N and 20.5086° E.

We found an estimated 450 individuals on the site, counting only the flowering individuals. The exact number of individuals is supposed to be at least two times higher, due to the species life-form trait.

Habitat characterisation of the locality

Gyűr Hill is a typical example of former land use in the Bükk foothills. Small patches of cultivated land (especially orchards with the well-known black fruited cultivar of “Szomolya cherry”) and abandoned parcels coexist with noteworthy remnants of natural vegetation patches (semidry grasslands and thickets). The habitat of *Campanula macrostachya* is situated next to a cherry tree orchard on a dry grassland sparsely covered by thermophile shrubs (*Figure 3*).

The extent of the locality where the *Campanula macrostachya* individuals grow is approximately 0.2 hectares. The size of the grassland – thicket patches among the cultivated pieces of land – is rather small, altogether less than 2 hectares. According to historical maps, formerly the site was probably also an orchard and/or vineyard. The grassland is not uniform in terms of dominant grasses and herbs; the patchy structure of areas dominated by different herb and forb species is remarkable. The bedrock is a volcanic tuff (belonging to Harsány Rhyolite Tuff Formation, Pelikán 2005), the topsoil layer is rather shallow.

The species composition of the locality belongs to the *Cirsio pannonicae-Brachypodion* Hadač et Klika alliance, but closer vegetation syntaxon is not possible to determine. Altogether 41 species occur in the three relevés (*Table 1*). The shrubby patches are mostly formed by *Prunus spinosa*, *Rosa canina* s.l. and *Crataegus monogyna*, but along verges, notable stands of *Amygdalus nana*, *Rosa gallica*, *Acer tataricum* and *Cydonia oblonga* as a remnant of cultivation exist. The presence and expansion of the invasive *Robinia pseudo-acacia* is the most significant threatening factor on the site. The cover of grasses is rather variable, *Danthonia alpina*, *Bothriochloa ischaemum* and *Calamagrostis epigeios* being the most abundant species. The latter two grasses indicate degradation on the

locality, but also take part in the natural regeneration phase in secondary succession (Baráth 1963).



Figure 3. Habitat of *Campanula macrostachya* at village of Szomolya village (7 July 2015) (photo of A. Schmotzer).

Grasses with lower abundance and cover are also observed (an asterisk (*) indicates species which occur outside of the relevés), such as *Koeleria cristata*, *Festuca valesiaca**, *Poa angustifolia*, *Helictotrichon compressum**, *Bromus japonicus*, *B. hordeaceus**, *Alopecurus pratensis*, *Elymus repens* and *Ventenata dubia*. The core of the grassland is formed by generalist *Festuco-Brometea* and *Festucetalia* species, e.g. *Fragaria viridis*, *Galium verum*, *Potentilla recta*, *Pseudolysimachion orchideum*, *Trifolium montanum*, *T. alpestre*, *Dorycnium herbaceum*, *Verbascum phoeniceum**, *Orchis morio**, *Vinca herbacea**. Tall-herb forbs and forest fringe dicots have a significant role in natural secondary succession, and are represented in the locality mostly by *Asteraceae* and *Apiaceae* species, such as *Aster linosyris*, *Inula ensifolia*, *I. salicina*, *I. hirta**, *I. germanica**, *I. oculus-christi**, *Centaurea scabiosa**, *Peucedanum alsaticum*, *P. cervaria* * and *Seseli osseum*. The presence of typical,

regionally broadly distributed perennials (e.g. *Artemisia pontica**, *Thlaspi jankae**, *Lychnis coronaria**, *Ornithogalum brevistylum*, *Ranunculus pedatus**) and annual steppe species (e.g. *Androsace elongata**, *Xeranthemum cylindraceum*, *Tordylium maximum*, *Crepis pulchra**, *Valerianella dentata*) is also characteristic. The successional trend probably leads to the regeneration of the semi-natural *Danthonia alpina* or *Stipa* spp. dominated grasslands, or the shrubby phase of the vegetation may be strengthened and a secondary, partly closed forest may develop.

Table 1. Floristic composition of the patch with *Campanula macrostachya*.

Nr. of relevé	1	2	3	Freq.
Cover of shrub layer in %	–	20	–	
Cover of herb layer in %	76	93	85	
Height of shrubs in cm	–	80-120	–	
Height of herbs in cm	20-45	30-60	30-120	
Species number	26	26	18	
- Shrub layer -				
<i>Prunus spinosa</i>		16		1
<i>Rosa canina</i> s.l.		4		1
- Herb layer -				
<i>Arenaria serpyllifolia</i>	a	a	0.5	3
<i>Bromus japonicus</i>	+	1	1	3
<i>Campanula macrostachya</i>	0.5	3	0.5	3
<i>Danthonia alpina</i>	1	2	60	3
<i>Fragaria viridis</i>	15	15	8	3
<i>Galium verum</i>	5	5	5	3
<i>Peucedanum alsaticum</i>	25	3	3	3
<i>Potentilla recta</i>	5	6	1	3
<i>Prunus spinosa</i>	6	15	+	3
<i>Pseudolysimachion orchideum</i>	0.5	2	+	3
<i>Xeranthemum cylindraceum</i>	5	30	0.5	3
<i>Aster linosyris</i>	6	6		2
<i>Cerastium brachypetalum</i>	+	+		2
<i>Dorycnium herbaceum</i>	+	2		2
<i>Koeleria cristata</i>	1		0.5	2
<i>Lathyrus nissolia</i>	a	a		2
<i>Lepidium campestre</i>		+	+	2
<i>Poa angustifolia</i>	+	2		2
<i>Valerianella dentata</i>	+		+	2

Accompanying, accidental species (with the relevé number in brackets): *Alopecurus pratensis* 1 (2), *Arabis glabra* a (1), *Bothriochloa ischaemum* 1 (3), *Crataegus monogyna* 3 (1), *Elymus repens* + (3), *Falcaria vulgaris* a (2), *Hypericum perforatum* + (2), *Inula ensifolia* 0,5 (3), *I. salicina* + (1), *Lathyrus tuberosus* + (1), *Ornithogalum brevistylum* + (1), *Odontites lutea* 3 (3), *Rosa canina* s.l. a (2), *Seseli osseum* 1 (1),

Tordylium maximum a (2), *Torilis arvensis* a (2), *Trifolium montanum* 1 (1), *Ventenata dubia* a (1), *Veronica arvensis* + (2), *Vicia angustifolia* a (2).

Relevés made by: András Schmotzer and Jana Tábořská, Date: 07.07.2016., Location: Hungary, Borsod-Abaúj-Zemplén county, Szomolya village. Position (centroid): 47.8896° N and 20.5086° E. Altitude: 230–235 m. Exposition: south. Declination: 2–5°. Plot size: 4 m².

Critical evaluation of the distribution of *Campanula macrostachya* in the Bükk Mts

As our investigation of herbarium specimens and literature data showed, *Campanula macrostachya* was reliably recorded before this present rediscovery in two localities in the Bükk Mts. Both localities are situated in the Bükk foothills. Some additional occurrence data were also included in this survey, but both are regarded erroneous, and neither herbarium specimens, nor precise literature data provision were added. The distribution map indicates the localities used in this chapter (Figure 4).

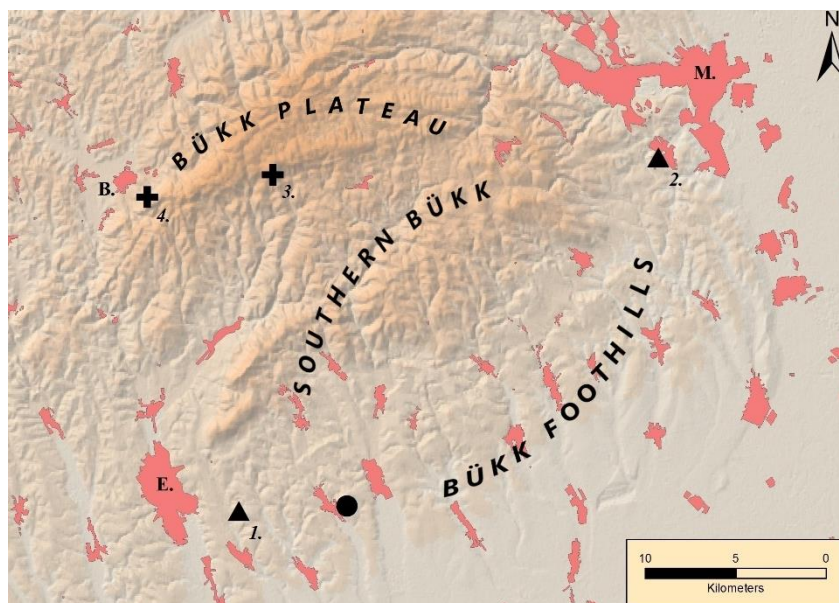


Figure 4. Distribution of *Campanula macrostachya* in the Bükk Mts. (Hungary): ▲ – confirmed historical locations; ● – recent location; ✚ – erroneous locations; E = Eger; M. = Miskolc; B. = Bélapátfalva; numbers are referring to the locations (see text) (compiled by A. Schmotzer).

Confirmed historical data

1. "Ostoros" (Heves County) – probable CEU grid: 8188/2.

The species was first reported from the Bükk by Gyula Prodán (1909). Unfortunately, he neglected to add detailed toponyms for his finding, only presented as "*C. macrostachya* W x K, on pastures in the vicinity of Ostoros". Nowadays no voucher specimen of this finding is known, but according to Samu Kupcsok, it was still available in 1912. He could have identified his *Campanula* sp. specimen collected at Bát village (Bátovce, Slovakia) as *C. macrostachya* based on a specimen that originated from Prodán's collection (Kupcsok 1912). Prodán's record was also quoted by Soó (1937) and Vojtkó (2001). Jávorka's note in his masterpiece Flora Hungarica could also refer to this data source, but he added the location as "at Eger town" (Jávorka 1925). The plant has not been found near Ostoros in the past decades, despite of intensive flora surveys that have taken place there (Pifkó and Barina 2004, Schmotzer 2015).

2. "Miskolctapolca" (Borsod-Abaúj-Zemplén County; also indicated as Görömbölytapolca, now belonging to the city of Miskolc) – probable CEU grids: 7990/2 or 7990/4.

Rezső Soó found the species in Miskolctapolca in 1938. The voucher specimen is deposited in the Herbarium Carpato-Pannonicum Budapest (BP; ID number. 394203). The authentic label text is "*Locus natalis cott. Borsod. mt. Bükk. in pratis siccis collinis pr. balneas G.Tapolca. 17.06.1938*". Later he also added this finding to the preliminary flora evaluation of the Bükk Mts (Soó 1943). He also indicated in this work that *Campanula macrostachya* occurred there in vast individual numbers ("*C. macrostachya* Kit. Tapolca! dry grassland on a slope of a hill; plenty"). Vojtkó (2001) also added this record to his work as a piece of literature data.

The exact locality is not known precisely, but the surroundings of the 'Miskolctapolca Thermal Spa' have changed a lot in the last seven decades. Continuous urbanisation has destroyed several natural grasslands there. We have carried out a sporadic floristic investigation in the surrounding areas, but no locality of *Campanula macrostachya* has been found. Several small patches of semi-natural vegetation still occur at Miskolctapolca among orchards and gardens (Sonkoly 2014, Schmotzer 2015), so existing populations might be lying hidden.

Erroneous data

3. “Tarkő” (Heves and Borsod-Abaúj-Zemplén County; belonging to Felsőtárkány or Szilvásvár)ad)

Only one piece of data was published from this location as “at Eger town and on Tarkő” in Flora Hungarica (Jávorka 1925, Vojtkó 2001). No voucher specimen or closer data source is known.

The location is regarded as unsuitable for this species. Tarkő Rock (945 m a.s.l.) – as a member of the characteristic rocky cliffs bordering the Bükk Plateau – is formed by cavernous Triassic limestone. *Campanula macrostachya* prefers lower altitudes and warmer conditions and its distribution is usually limited to volcanic or sediment bedrocks. The locality has been studied continuously by florists and there is no source proving the occurrence of the species there (Vojtkó 2001).

4. “Bélkő” (Heves County, belonging to Bélapátfalva)

This locality was presented only in a monograph on protected plant species occurring in Hungary (Farkas 1999). The primary data source was also not evident and was not included in the flora monograph of the Bükk Mts. (Vojtkó 2001).

The location has similar natural conditions to those of Tarkő Rock (limestone as bedrock and higher altitude), so we assume that this is also an erroneous report of the species.

CONCLUSIONS

The data presented indicate that the strictly protected *Campanula macrostachya* has only one recent location in the Bükk Mts. It has been found nearly 80 years after the last confirmed report. Two former pieces of historical occurrence data have been confirmed (Ostoros, Miskolcápolca). On the other hand we have found two locations which should be erroneous and possibly deleted from the enumeration of the species in the Bükk Mts. The closest site of *Campanula macrostachya* occurs westwards in the Mátra foothills at a distance of about 38 kilometres from the Szomolya locality. This population at Feldebrő village was found by Csaba Molnár in 2004 (the voucher specimen is in the Herbarium Carpato-Pannonicum Budapest (BP; ID number 669318; see also Sramkó et al 2008). The documented locality in Bükk foothills is found outside of protected area, so its conservation deserves special attention in the future. The

population is rather strong (assumed to be more than 500 individuals), but it is threatened by possible land use conversions (such as the creation of orchards and vineyards) and natural successional processes, especially black locust invasion.

Acknowledgements – The authors would like to thank our reviewers, Zoltán Barina and András Vojtkó (Eger) for their improvements to the manuscript. We are indebted to Zoltán Barina and Dániel Pifkó (Budapest; BP) for the herbarium assistance and to Verica Stojanović (Belgrade) for providing the Serbian literature concerning this species. The authors are grateful to Csaba Németh (Budapest) for photographing the voucher specimen. Thanks to Albert Vermes (Eger) who kindly improved the English of the revised version.

REFERENCES

- BALOGH, K. (1964). A Bükk hegység földtani képződményei. *A Magyar Állami Földtani Intézet Évkönyve* **48**(2): 245–719.
- BARÁTH, Z. (1963). Növénytakaró vizsgálatok felhagyott szőlőkben. (Analyses of vegetation cover in abandoned vineyards). *Földrajzi Értesítő* **2**(3): 341–356.
- BARINA, Z. (2004). A Dunántúli-középhegység növényföldrajzának főbb jellemzői. (Characteristics of the phytography of Transdanubian Mountains in Hungary.) *Flora Pannonica* **2**(2): 37–55.
- BARINA, Z. (2006). *A Gerecse hegység flórájának katalógusa*. (Flora of the Gerecse Mountains.). Magyar Természettudományi Múzeum – Duna-Ipoly nemzeti Park Igazgatóság, Budapest, 612 pp.
- BARINA, Z. (2014). Kitaibel Pál (1757–1817) és a 21. század – mitől lesz „élő” egy 200 éves herbárium? (A 200-year-old “living herbarium” – bringing botanist Pál Kitaibel (1757–1817) into the 21st century). *Annales historico-naturales Musei nationalis hungarici* **106**: 141–156.
- BARINA, Z., PIFKÓ, D. & SOMOGYI, G. (2016). The influence of Bruno Schütt (1876–1956) on Albanian floristic research. *Phytotaxa* **273**(1): 1–22.
- BARTHA, D., KIRÁLY, G., SCHMIDT, D., TIBORCZ, V., BARINA, Z., CSIKY, J., JAKAB, G., LESKU, B., SCHMOTZER, A., VIDÉKI, R., VOJTKÓ, A. & ZÓLYOMI, SZ. (2015). *Magyarország edényes növényfajainak elterjedési atlasza*. (Distribution atlas of vascular plants of Hungary.) Nyugat-magyarországi Egyetem Kiadó / University of West Hungary Press, Sopron, 329 pp.
- BÖHM, É. (2001). *Florisztikai vizsgálatok a Duna-Ipoly Nemzeti Park dél-délkeleti peremén*. (Floristical studies on the south-east edge of the Danube-Ipoly National Park (DINP), Hungary.) *Kitaibelia* **6**(1): 51–71.
- BOISSIER, E. (1875). *Flora orientalis sive Enumeratio plantarum in Oriente, a Graeca et Aegypto ad Indiae fines hucusque observatarum*. Vol. III. H. Georg, Geneva & Basilea (Basel), 1033 pp.
- BORHIDI, A., KEVEY, B. & LENDVAI, G. (2012). *Plant communities of Hungary*. Akadémiai Kiadó, Budapest, 544 pp.
- BRAUN-BLANQUET, J. (1932). *Plant sociology* (Transl. Fuller, G.D & Conrad, H.S.). McGraw-Hill, New York, 539 pp.

- CIOCĂRLAN, V. (2009). *Flora ilustrată a României. Pteridophyta et Spermatophyta*. Edit. Ceres, București, 1141 pp.
- DAMBOLDT, J. (1978). *Campanula*. In: DAVIS, P.H. (ed.): *Flora of Turkey and the East Aegean Islands*, vol. 6: 2–64. Edinburgh Univ. Press, Edinburgh.
- ELIÁŠ JUN., P., DÍTĚ, D., KLIMENT, J., HRIVNÁK, R. & FERÁKOVÁ, V. (2015). Red list of ferns and flowering plants of Slovakia, 5th edition (October 2014). *Biologia (Bratislava)* **70**(2): 218–228.
- EURO+MED (2006). Euro+Med PlantBase, the information resource for Euro-Mediterranean plant diversity. Published on the Internet <http://ww2.bgbm.org/EuroPlusMed/> [accessed 12.11.2016].
- FARKAS, S. (1999). *Magyarország védett növényei*. (Protected plants of Hungary). Mezőgazda Kiadó, 416 pp.
- FEDOROV, A.A. (1957). *Campanulaceae*. In: SHISHKIN B.K. (ed.): *Flora of the SSSR*. Moscow. Akademii Nauk SSSR, pp. 92–321.
- FEDOROV, A.A. & KOVANDA, M. (1976). *Campanula*. In: TUTIN, T.G., HEYWOOD, V.H., BURGESS, A., MOORE, D.M. & VALENTINE, D.H. & al. (eds.): *Flora Europaea*. Cambridge: Cambridge University Press, pp. 74–93.
- FEKETE, G., MOLNÁR, ZS, MAGYARI, E., SOMODI, I., VARGA, Z. (2011). Egyediség, szabályszerűség és deviáció a Pannon Régió vegetációjának példáján. (Individualities, regularities and deviations: example of the vegetation in the Pannonian Region.). *Botanikai közlemények* **98**(1-2): 29–59.
- FINTHA, I. (1994). *Az Észak-Alföld edényes flórája*. TermészetBúvár Alapítvány Kiadó, Budapest, 130 pp.
- GOLIAŠOVÁ, K., MICHÁLKOVÁ, E. & MRÁZ, P. (2008). *Campanula* L. In: GOLIAŠOVÁ, K. & ŠÍPOŠOVÁ, H. (eds.). *Flóra Slovenska VI/1*. Veda, Vydavateľstvo SAV, Bratislava, pp. 276–279.
- HOLUB, J. (1999). *Campanula macrostachya*. In: ČEROVSKÝ, J., FERÁKOVÁ, V., HOLUB, J., MAGLOCKÝ, Š. & PROCHÁZKA, F. (eds.): *Červená kniha ohrozených a vzácných druhů rostlin a živočichů ČR a SR*. Vol. 5. Vyšší rostliny [Red Data Book of threatened plants and animals of the Czech Republic and Slovak Republic. Vol. 5. Higher plants]. Příroda, Bratislava. p. 70.
- JÁVORKA, S. (1925). *Magyar Flóra (Flora Hungarica)*. Studium Kiadása, Budapest, 1307 pp.
- KIRÁLY, G. (2003). A magyarországi flóratérképezés módszertani alapjai. Útmutató és magyarázat a hálótérképezési adatlapok használatához. (Methodik und Ziele der Florenkartierung in Ungarn). *Flora Pannonica* **1**(1): 3–20.
- KIRÁLY, G. (ed., 2007). *Vörös Lista. A magyarországi edényes flóra veszélyeztetett fajai*. (Red list of the vascular flora of Hungary). Sajat kiadás, Sopron, 73 pp.
- KIRÁLY, G. (ed., 2009). *Új magyar fűvészkönyv. Magyarország hajtásos növényei. Határozókulcsok*. (New Hungarian Herbal. The vascular plants of Hungary). Aggteleki Nemzeti Park Igazgatóság, Jósvafő, 616 pp.
- KONDRACKI, J. (1978). *Karpaty, Wydawnictwo Szkolne i Pedagogiczne*. Warsaw.
- KOVAČIĆ, S. (2004). The genus *Campanula* L. (Campanulaceae) in Croatia, circum-Adriatic and west Balkan region. *Acta Bot. Croat.* **63**(2): 171–202.
- KOVÁTS, D. (1992). Waldstein and Kitaibel types in the Hungarian Natural History Museum in Budapest. *Annales historico-naturales Musei nationalis hungarici* **84**: 33–53.

- KOŽUHAROV, S.I. & ANCHEV, M.E. (eds., 2012). *Florae Reipublicae Bulgaricae*. Vol. 11. Editio Academica "Professor Marin Drinov", Serdicae, 523 pp.
- KUPCSOK, J. (1912). *Campanula macrostachya*. *Magyar Botanikai Lapok* **11**: 282.
- MALATINSZKY, Á., MRAVCSIK, Z. & DEDÁK, D. (2014). Florisztikai adatok a Cserhát felhagyott szőlőiből. (Floristical data from abandoned vineyards of Cserhát Hills.). *Kitaibelia* **19**(2): 260–266.
- MARHOLD, K. & HINDÁK, F. (eds., 1998). *Checklist of non-vascular and vascular plants of Slovakia*. VEDA, Bratislava, 688 pp.
- MEUSEL, H. & JÄGER, E.J. (1992). *Vergleichende Chorologie der zentraleuropäischen Flora*. Text u. Karten. Bd. 3., Gustav Fischer Verlag Stuttgart New York, 688 pp.
- MICHÁLKOVÁ, E. (2007). *Campanula macrostachya* Waldst. et Kit. ex Willd. (*Campanulaceae*). In: MRÁZ, P. (ed.): *Chromosome number and ploidy level reports from Central Europe*. 3. Reports (33–34), *Biologia (Bratislava)* **62**: 507–510.
- NAGY, J. (2007). *A Börzsöny hegység edényes flórája*. (Vascular flora of the Börzsöny Mountains). Rosalia 2. Duna-Ipoly Nemzeti Park Igazgatóság, Budapest, 378 pp.
- NIKLFIELD, H. (1971). Bericht über die Kartierung der Flora Mitteleuropas. *Taxon* **20**(4): 545–571.
- OBRADOVIĆ, M. (1974). *Campanulaceae* A. L. Juss. In: JOSIFOVIĆ, M. (ed.): *Flora SR Srbije*. 6. Srpska Akademija Nauka i Umetnosti. Beograd. VI/1. pp. 528–573.
- OPREA, A. (2005). *Lista critică a plantelor vasculare din România*. Edit. Univ. „Al. I. Cuza”, Iași: 488 pp.
- PELIKÁN, P. (ed., 2005). *Geology of the Bükk Mountains: explanatory book to the Geological map of the Bükk Mountains (1:50 000)*. Budapest, Magyar Állami Földtani Intézet, 284 pp.
- PIFKÓ, D. & BARINA, Z. (2004). Adatok a Bükkalja flórájához. (Floristic data of the territory of the "Bükkalja" region (N-Hungary)). *Kitaibelia* **9**(1): 151–164.
- PRODÁN, Gy. (1909). Adatok a Bükk- és előhegyeinek flórájához. *Botanikai közlemények* **8**(3): 103–117.
- SAG, G. & GOTTHARD, D. (1985). Plantes de Hongrie étrangères à la flore française et leur répartition, Bulletin de la Société Botanique de France. *Lettres Botaniques* **132**(4-5): 349–358.
- SCHMOTZER, A. (2015). *Ceratocephala testiculata* (Crantz) Roth és további adatok a Bükkalja flórájához. (*Ceratocephala testiculata* (Crantz) Roth and further data to the flora of the foothills of Bükk Mts. ('Bükkalja', NE Hungary)). *Kitaibelia* **20**(1):81–142.
- SHABANOVA, G.A., IZVERSKAYA, T.I. & GHENDOV, V.S. (2014). *Flora and Vegetation of Bujac Steppes of the Republic of Moldova*. Chisinau. Eco-TIRAS, 324 pp.
- SONKOLY, J. (2014). Adatok Miskolc és a Bükk hegység flórájának ismeretéhez. (Floristic data from Miskolc and the Bükk Mountains (N Hungary)). *Kitaibelia* **19**(2): 267–274.
- Soó, R. (1937). *A Mátrahegység és környékének flórája*. Magyar Flóraművek I. Debrecen, 89 pp.
- Soó, R. (1943). Előmunkálatok a Bükkhegység és környéke flórájához. *Botanikai közlemények* **40**: 169–221.
- Soó, R. (1968). *A magyar flóra és vegetáció rendszertani-növényföldrajzi kézikönyve*. (Synopsis systematico-geobotanica florae vegetationsisque Hungariae). Akadémiai Kiadó. Budapest, Vol. 3. pp. 449–450.

- SRAMKÓ, G., MAGOS, G., MOLNÁR, CS. & URBÁN, L. (2008). Adatok a Mátra és környéke edényes flórájának ismeretéhez. (Data to the knowledge of the vascular flora of the Mátra Mountains and its surroundings). *Kitaibelia* **13**(1): 74–93.
- SÜTŐ, L., MCINTOSH, R.W., HEVESI, A. & VERESS, M. (2015). *Bükk Plateau: A Karst Landscape*. In: LÓCZY, D. (ed.): *Landscapes and Landforms of Hungary*. Springer International Publishing, pp. 189–199.
- TAKÁCS, A., NAGY, T., FEKETE, R. LOVAS-KISS, Á., LJUBKA, T., LÖKI, V., LISZTES-SZABÓ, ZS. & MOLNÁR, V.A. (2015a). A Debreceni Egyetem Herbáriuma (DE) I.: A „Soó Rezső Herbárium”. (The herbarium of Debrecen University (DE) I. The “Rezső Soó Herbarium”). *Kitaibelia* **19**(1): 142–155.
- TAKÁCS, A., SÜVEGES, K., LJUBKA, T., LÖKI, V., LISZTES-SZABÓ, ZS. & MOLNÁR, V.A. (2015b). A Debreceni Egyetem Herbáriuma (DE) II.: A „Siroki Zoltán Herbárium” (The Herbarium of Debrecen University (DE) II.: The „Zoltán Siroki Herbarium”). *Kitaibelia* **20**(1): 15–22.
- TEOFILOVSKI, A. (2011). *Contributions to the flora of the Republic of Macedonia*. Skopje, 142 pp.
- TURIS, P., KLIMENT, J., FERÁKOVÁ, V., DÍTĚ, D., ELIÁŠ, P., HRIVNÁK, R. KOŠTÁL, J., ŠUVADA, R., MRÁZ, P. & BERNÁTOVÁ, D. (2014a). Red List of vascular plants of the Carpathian part of Slovakia. *Thaiszia – Journal of Botany* **24**(1): 35–87.
- TURIS, P., ELIÁŠ, P., SCHMOTZER, A., KIRÁLY, G., SCHNEIDER, E., KUCIEL, H., SZEWCZYK, M., KOZURAK, A., ANTOSYAK, T., VOLOSCHCHUK, M., LAZAREVIĆ & LUSTYK, P. (2014b). *Red list of vascular plants of the Carpathians*. In: KADLEČÍK, J. (ed.): *Carpathian red list of forest habitats and species* (Draft). The State Nature Conservancy of the Slovak Republic, pp. 44–105.
- VOJTKÓ, A. (2001). *A Bükk hegység flórája*. (Flora of the Bükk Mountains). Sorbus 2001, Eger, 340 pp.
- WALDSTEIN, F. A. & KITAIBEL, P. (1811). *Descriptiones et Icones Plantarum Rariorum Hungariae*. Viennae, Volume 3, pp. 222–310.
- WILLDENOW, D. C. L. (1809). *Enumeratio Plantarum Horti Regii Botanici Berolinensis*. Libraria Scholae realis, Berolini, 1099 pp.
- WINTERL, J.J. (1788). (facsimile: 1972). *Index Horti Botanici Universitatis Hungaricae, quae Pestini est*. Pest, 161 pp.
- WITKOWSKI, Z.J., KRÓL, W. & SOLARZ, W. (eds., 2003). *Carpathian list of endangered species*. WWF and Institute of Nature Conservation, Polish Academy of Sciences, Vienna-Krakow.

(submitted: 17.11.2016, accepted: 14.12.2016)

LIGHT MICROSCOPIC STUDY OF *PORELLA PLATYPHYLLA* (L.) PFEIFF. CELLS UNDER VARIOUS ABIOTIC STRESS FACTORS

Szidónia Sütő & Marianna Marschall*

*Eszterházy Károly University, Institute of Biology,
Department of Botany and Plant Physiology, H-3300 Eger, Leányka u. 6, Hungary;
E-mail: marschall.marianna@uni-eszterhazy.hu

Abstract: The leaf cells of the extremely desiccation tolerant leafy liverwort, *Porella platyphylla* can be studied natively by light microscope due to their one-cell layered structure. The effects of various abiotic stress factors can be also monitored at cell level following the rate of plasmolysis, and the changes in the structure of cell organelles (chloroplasts, vacuoles, oil bodies). Furthermore our aim was to test the applicability of different stains (neutral red, toluidine blue, methylene blue, Sudan-III) in *Porella platyphylla* cells under experimental treatments. Natural drying at room temperature (for 1 day, 1 week, '62 years' by checking an old herbarium sample), subsequent rehydration, freezing at -18 and -80°C, heat treatment at 40, 50 and 100°C (for 5 and 10 min), osmotic and salt stress (0.5 M NaCl, 1 M KSCN, 25% PEG8000) were applied. In the course of monitoring the various stress factors the use of neutral red (at pH 7.6) staining proved to be the most optimal. In control plants one big cherry coloured vacuole was discovered after staining. The central vacuole fragmented into small pieces, then ruptured after 10 minutes, due to the strongest osmotic treatment (1 M KSCN). At the same time chloroplasts were irreversibly disrupted. The oil bodies proved to be the most resistant structures against the various stress factors. Plants hardened for 5-month-long cold were able to regenerate their cell structure and metabolism within 24 hours after a 1-day natural drying. The 3 different high temperature treatments (40, 50, 100°C) resulted in similar changes in the cell structure to those induced by the cold treatments. Tissues were coloured by neutral red before freezing and heat treatments suffered less injury compared with the unstained ones. Light microscopic studies are convenient to monitor the regeneration of the cell structure after stress.

Keywords: *Porella platyphylla*, liverworts, abiotic stress, desiccation, cytological structure, oil bodies

INTRODUCTION

Studies have shown that major cytological changes take place in mosses during drying-rewetting cycles (Pressel *et al.* 2006, Proctor *et al.* 2007a, b) and that these changes occur on a timescale reflected by the physiological events, although comparable information on the effects of de- and rehydration in liverwort vegetative cells is scarce (Marschall and Proctor 1999). In the same experimental design Pressel *et al.* 2009 described the physiological effects in six desiccation-tolerant (DT) liverworts and the cytological effects of drying and rewetting in two liverworts and examined parallels with and differences from vascular plants and mosses. In their work ultrastructural changes upon water stress and recovery were observed, using light and electron microscopy. Although some of the DT liverworts are well suited for physiological studies (for example *Porella platyphylla*), they are unsuitable for proper fixation and embedding for electron microscopy and, therefore, for answering the cytological questions posed in this study. Cytological changes associated with drying and rehydration in liverworts closely parallel those in mosses. Dehydration elicits profound cytological changes: fragmentation of the vacuole, and rounding of the chloroplasts and mitochondria, with the thylakoids and cristae remaining undamaged (Pressel *et al.* 2009). These changes closely parallel those seen in mosses and desiccation-tolerant vascular plants, as photosynthetic activity recovers to unstressed value after 24–48 h. As in mosses, in liverworts de- and rehydration are associated with the de- and repolymerization of the cortical microtubule cytoskeleton.

Liverworts are probably the earliest-diverging group of green land plants. Particularly interesting, liverworts contain unique membrane-bound organelles, the oil bodies. Oil bodies are fundamentally different in both substructure and development from lipid droplets, oleosomes, or sphaerosomes, which are common features throughout land plants (Duckett 1986), especially in storage tissues. Unlike lipid droplets (which lack a bounding membrane), the oil bodies of liverworts are bound by a single unit membrane and contain lipid globules suspended in a carbohydrate matrix (Galatis *et al.* 1978, Duckett and Ligrone 1995). The unusual chemical components of liverworts are generally considered to be concentrated in the oil bodies (Müller 1906, Suire 1975, Suire *et al.* 2000) and consist of highly diversified mixtures of terpenoids or

aromatic constituents (Asakawa 1995) in the lipid globules, fructans and polyols (such as mannitol, sorbitol, and volemitol) in the matrix (Smirnoff 1992, Marschall *et al.* 1998). There is a great relevance in liverwort taxonomy of observing and typing oil bodies (Kis and Pócs 1997, Sass-Gyarmati 2015). The biogenesis, their detailed constituents, the possible biological function of oil bodies in stress tolerance (i. e. in DT) is still unclear (Gavaudan 1927, Chalaud 1931, Pressel *et al.* 2009, He *et al.* 2013). Light microscopic investigations by bryologists have confirmed that (1) oil bodies rapidly disappear from herbarium specimens of most liverworts, (2) some species that grow under xeric conditions lack them altogether, and (3) they are as prominent in submerged aquatics as in highly DT taxa (Pressel *et al.* 2009). In the dry state, these remain substantially unchanged, but after rewetting, they become flattened and regain their normal morphology only after 48 h. When subjected to unnaturally fast rate of drying, the oil bodies, together with other organelles, disintegrate on rewetting. However, there is considerable variation between species in the length of time that a plant retains its oil bodies after collection (Paton 1999), and this seems to depend on its level of DT (Stewart 1978, Pressel *et al.* 2009). Retention of the oil bodies is firmly determined by the rate of water loss, which in turn depends on the habitat of the plant. Presumably, the oil bodies may have a crucial role in stress tolerance. The first land plant remains, fossil findings look like recent liverworts, which evolved approximately 760 million years ago (Kenrick and Crane 1997, Wellman *et al.* 2003, He-Nygrén *et al.* 2004, Qiu *et al.* 2006, Rubinstein *et al.* 2010). The chemical constituents of leafy liverworts' oil bodies seem to protect the plant from the pathogens, herbivores, cold temperature and strong light (Hieronymus 1892) and, in addition, from the excessive UV radiation and the desiccation too (Gavaudan 1927, Chalaud 1931, Pressel *et al.* 2009). Marschall *et al.* (1998) and Pressel *et al.* (2009) provided the first experimental evidence that the oil bodies may have a crucial role in the metabolism of desiccation tolerance by suggesting a shifting of soluble carbohydrates or other moieties into the cytosol. Desiccation caused a decrease in sucrose and total fructan (the major components of the soluble carbohydrate pool of *Porella platyphylla*) but an increase in the proportion of high-molecular weight fructan, leading the authors to suggest that polymerization occurred during drying. Marschall *et al.* (1998) further argued that, although the fate of soluble carbohydrates

during tissue drying was not investigated, some of them appeared to be converted to an insoluble form or to a noncarbohydrate such as terpenoids in the oil bodies and that oil bodies could act as a store of carbon to buffer the soluble carbohydrate pool.

The aim of this study was to provide more information of the cytological changes associated with abiotic stress factors and recovery mechanisms using light microscopy in a desiccation tolerant leafy liverwort (*P. platyphylla*), focusing particular attention on the behaviour of the oil bodies. The effects of various abiotic stress factors such as natural drying and subsequent rehydration, freezing at -18 and -80°C, heat treatment at 40, 50 and 100°C (for 5 and 10 min), osmotic and salt stress (0.5 M NaCl, 1 M KSCN, 25% PEG8000) were monitored at cell level following the rate of plasmolysis, and the changes in the structure of cell organelles (chloroplasts, vacuoles, oil bodies). Furthermore our aim was to test the applicability of different stains (neutral red, toluidine blue, methylene blue, Sudan-III) in *Porella platyphylla* cells, to make more profoundly visible the cytological changes during monitoring the effect of the different abiotic stress factors.

MATERIALS AND METHODS

Plant material

Porella platyphylla (L.) Pfeiff. is a DT leafy liverwort and was collected from an area of limestone woodland in the Bükk Mountains, north-east Hungary, near Felsőtárkány village in autumn and winter in 2013. The plant mostly appears in northerly exposed tree-shaded sites, and can usually be found on limestone rocks, but can also appear on tree-trunks. The plants were at their full turgor when they were collected. Until the experiments plants were kept in fully hydrated states (no longer than 3 days) in plastic boxes in a fridge at 5°C.

Dying techniques

Different cell stains (neutral red at pH 2.1, 4.7, and 7.6, toluidine blue, methylene blue, Sudan III) were used to test their applicability in *P. platyphylla* leaves during monitoring the effects of the various abiotic stress factors.

Experimental treatments

Natural drying and rehydration

In autumn and winter, freshly collected plants at full turgor were allowed to dry for 1 day in the laboratory at 24 °C, RH 35-40% and PPFD of 100 $\mu\text{mol m}^{-2}\text{s}^{-1}$. This process resulted in slow drying of the liverworts. After the drying, rehydration was achieved by immersing the plants in distilled water. After remoistening constant hydration status was maintained in glass desiccators containing distilled water. The changes in the cell structure were monitored by light microscopy after 0, 10, 30, 40 min, 1h, 24h and 48h following rehydration.

A 62-year-old herbarium sample of *P. platyphylla*, which was collected at Felsőtárkány in 1953, was remoistened with distilled water, methylene blue and neutral red (at pH 2.1, 4.7, 7.6) stains and the cell structure was studied by light microscopy 0 and 30 min after rehydration.

Cold treatment in dark

Autumn samples were kept at full turgor in 5°C for 5 months in dark. After the cold treatment samples were allowed to dry for 1 day in the laboratory at 24 °C, RH 35-40% and PPFD of 100 $\mu\text{mol m}^{-2}\text{s}^{-1}$. After drying, rehydration was achieved by immersing the plants in distilled water. After remoistening constant hydration status was maintained in glass desiccators containing distilled water. The changes in the cell structure were monitored by light microscopy after 0, 10, 30, 40 min, 1 h, 24 h and 48 h following rehydration. In another case, the samples were taken in winter and were then subjected to dehydration for 1 day at laboratory air. Rewetting was carried out with distilled water and monitoring of the cells was done at the same time intervals as in the autumn samples.

Freezing

The plant samples were frozen at -18°C and -80°C for 5 days. Neutral red staining (pH 7.6) was applied before as well as after the freezing treatment.

Heat treatment

Unstained and neutral red (pH 7.6) stained plants were subjected to heat treatments at 40, 50 and 100°C for 5 and 10 min. Heat treatments were carried out in a water-bath.

Osmotic and salt stress

Neutral red (pH 7.6) stained plants were subjected to the following osmotic and salt stress for 3 hours: 25% PEG8000 ($\Psi_s = -1.435$ MPa), 0.5 M NaCl ($\Psi_s = -2.318$ MPa) and 1 M KSCN ($\Psi_s = -4.381$ MPa).

Light microscopic studies

The cells of *Porella platyphylla* leaves were studied natively by light microscope due to their one-cell layered structure. The cytological changes that resulted from the various abiotic stress factors applied were monitored with an Olympus CX 40 type of light microscope, and the recordings were taken by an Olympus DP12 microscope camera.

RESULTS AND DISCUSSION

Methylene blue stain

The cells of *Porella platyphylla* leaves are uniform. Methylene blue stain coloured the cell walls in the leaf cells of *Porella platyphylla* at full turgor and the colour of the cytoplasm changed to light blue due to methylene blue linking to objects with acidic character (*Photo 1a*). Lots of oval chloroplasts and shiny homogeneous oil bodies are visible in turgid cells. Oil bodies in *P. platyphylla* are small, numerous, and not very distinct. Moreover, like many other DT liverworts, *P. platyphylla* is extremely difficult to infiltrate with resin (Duckett *et al.* 1988), the improminent oil bodies do not fix and embed well for electron microscopy (Duckett *et al.* 2006a, 2006b), therefore views we get by light microscopy could be important and valuable.

In the 62-year-old herbarium sample the membrane structure disintegrated, cells could not regenerate upon rehydration. Oil bodies were disrupted, methylene blue stained the remaining parts of chloroplasts structure (*Photo 1b*).

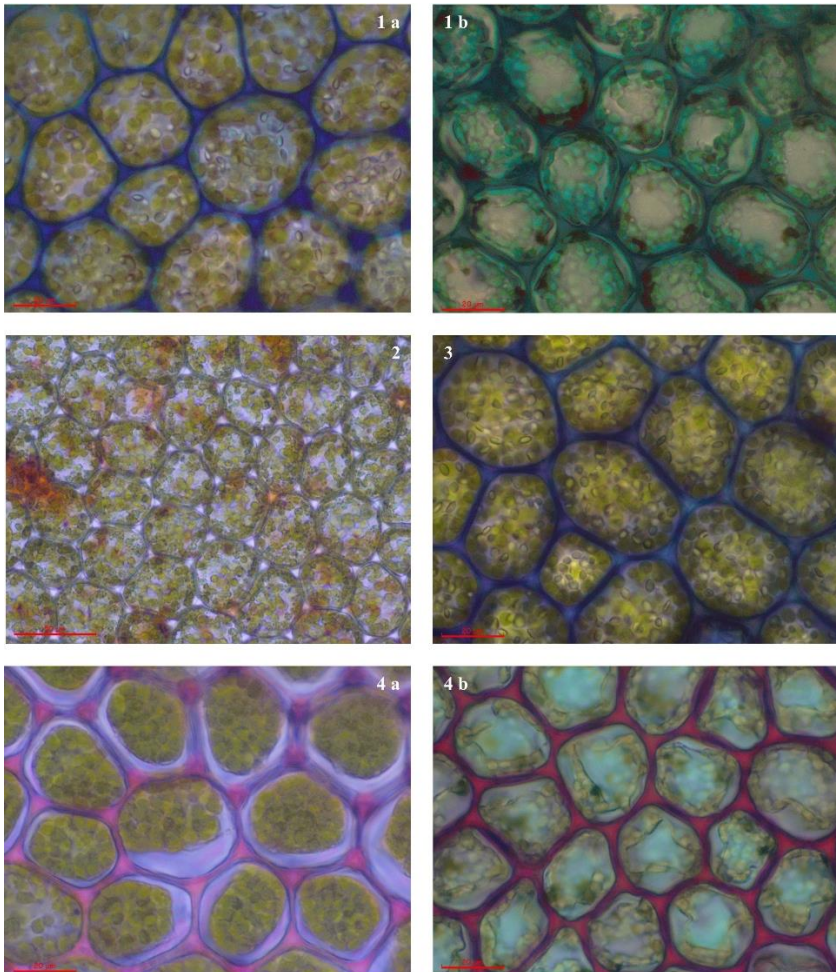


Photo 1a, b. a) Leaf cells of *P. platyphylla* at full turgor stained by methylene blue. b) Dead leaf cells of a 62-year-old (a herbarium sample) *P. platyphylla* were re moistened and stained by methylene blue. Photo was taken 30 minutes after rehydration. Scale bars = 2 μ m. **Photo 2.** The result of applying Sudan III in the leaf cells of *P. platyphylla* at full turgor. Scale bar = 2 μ m. **Photo 3.** Leaf cells of *P. platyphylla* at full turgor stained by toluidine blue. Scale bars = 2 μ m. **Photo 4a, b.** *P. platyphylla* leaf cells a) at full turgor b) in the 62-year-old herbarium sample were stained with neutral red at pH 2.1. Scale bars = 2 μ m.

Sudan III stain

The Sudan III stain is widely used for microscopy procedures in plant tissues which have large oil content. Using Sudan III neutral fats (lipids) are coloured red. The reason why we tried this staining

on *P. platyphylla* is that we wanted to see whether oil bodies were coloured or not. The method was not suitable for *P. platyphylla*. The relatively high alcohol content of Sudan III significantly damaged the liverwort cells (*Photo 2*) and the oil bodies too. On the other hand, it can't be excluded that the oil bodies of *P. platyphylla* do not contain neutral lipids where the stain could be linked.

Toluidine blue stain

Applying alcalic aniline stain, the toluidine blue, the cell walls are coloured purple blue and the cytoplasm light violet (*Photo 3*).

Neutral red staining at different pH-s

In *P. platyphylla* leaf cells at full turgor the cell walls were stained reddish pink with neutral red at pH 2.1. At this pH the cells suffered convex plasmolysis, cell membrane separated from the cell wall. Oil bodies could not be observed, and the other organelles were degraded, for example the chloroplasts, their content formed green grist. The vacuoles were not stained (*Photo 4a*). The cell walls of a 62-year-old herbarium leaf sample were also painted reddish pink (*Photo 4b*).

In *P. platyphylla* leaf cells at full turgor the cell wall, cytoplasm and vacuoles were coloured dark blue/scarlet with neutral red at pH 4.7. The membranes and the organelles remained safe and sound after the staining at pH 4.7, so this pH did not have a destructive effect on the cell structure (*Photo 5a*) The cell walls and some remaining parts of organelles of the 62-year-old herbarium leaf sample were also painted reddish pink (*Photo 5b*).

Applying neutral red at pH 7.6 in *P. platyphylla* leaf cells at full turgor, the vacuoles were coloured red intensively due to the neutral red cationic trapping mechanism, cell walls were not stained (*Photo 6a*). Using neutral red at pH 7.6 was found to be the most suitable staining for studying the effects of various abiotic stress factors in *P. platyphylla* leaf cells by light microscopy. In the old herbarium leaf sample only the cell walls were coloured light pink (*Photo 6b*).

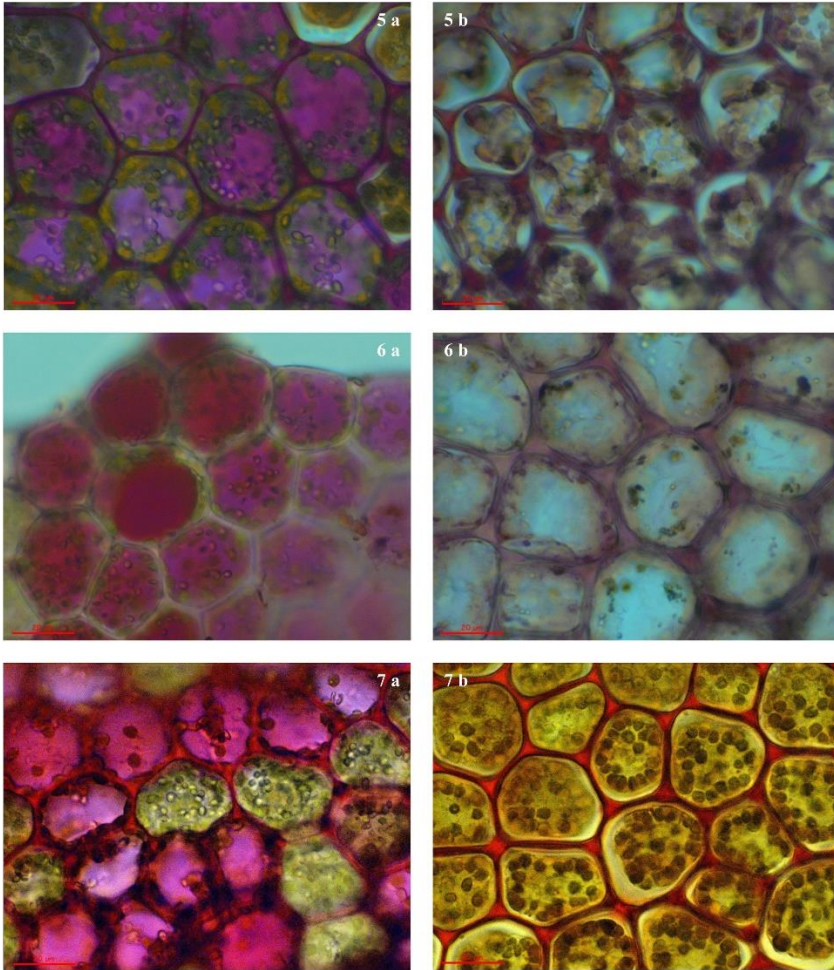


Photo 5a, b. *P. platyphylla* leaf cells a) at full turgor b) in the 62-year-old herbarium sample were stained with neutral red at pH 4.7. Scale bars = 2 μm . **Photo 6a, b.** *P. platyphylla* leaf cells a) at full turgor b) in the 62-year-old herbarium sample were stained with neutral red at pH 7.6. Scale bars = 2 μm . **Photo 7a, b.** *P. platyphylla* leaf cells at full turgor were frozen at a) -18°C and b) -80°C . Before freezing neutral red staining was applied at pH 7.6. Scale bars = 2 μm .

The effect of freezing at -18 and -80°C

Before freezing at -18 and -80°C *P. platyphylla* leaf cells at full turgor were stained with neutral red at 7.6 pH. At both freezing temperatures the organelles were damaged and dispersed around in the cytoplasm (*Photo 7a, b*). Freezing at -18°C resulted in more

visible damage symptoms in the cell structure than freezing at -80°C . The reason for this is that the longer and slower freezing process could cause the formation of large ice crystals which destroy membrane systems and organelles too. Cells were unimpaired after the rapid and short frost effect at -80°C . When the cells were coloured with neutral red before freezing, the melting process had less harmful effect on the cell structure. The water vapour is responsible for the destructive effects inside the cells. In many instances the cells are damaged more during the melting process as during the freezing. Staining before freezing could have a protective role during melting. The chloroplasts were visible in their original structural arrangement, but they became a little bit bigger and deformed than in the control samples. Vacuoles could't be observed in the tissues after the treatment.

Applying colouring after the freezing of the *Porella* samples at -18°C , the cells were disintegrated, and the cytoplasm effused. The chloroplasts were damaged; they lost their structure and aggregated near the cell walls, peripherally. The oil bodies were not visible in their original state (*Photo 8a*).

When we applied staining after the freezing of the *P. platyphylla* samples at -80°C the cells plasmolyzed, chloroplasts disintegrated and became granulose, but they did not aggregate peripherally, and the cell membrane seemed to be intact (*Photo 8b*). The reason why the cell walls were painted with neutral red at pH 7.6 is because membranes, tonoplasts were disrupted upon freezing and the acidic character of vacuole could be released and could alter the pH of the neutral red stain. The molecular form of the neutral red turned to be positively charged. The cations of the neutral red could adsorb at the negatively charged sites of the cell walls in both freezing treatments (*Photo 8a, b*).

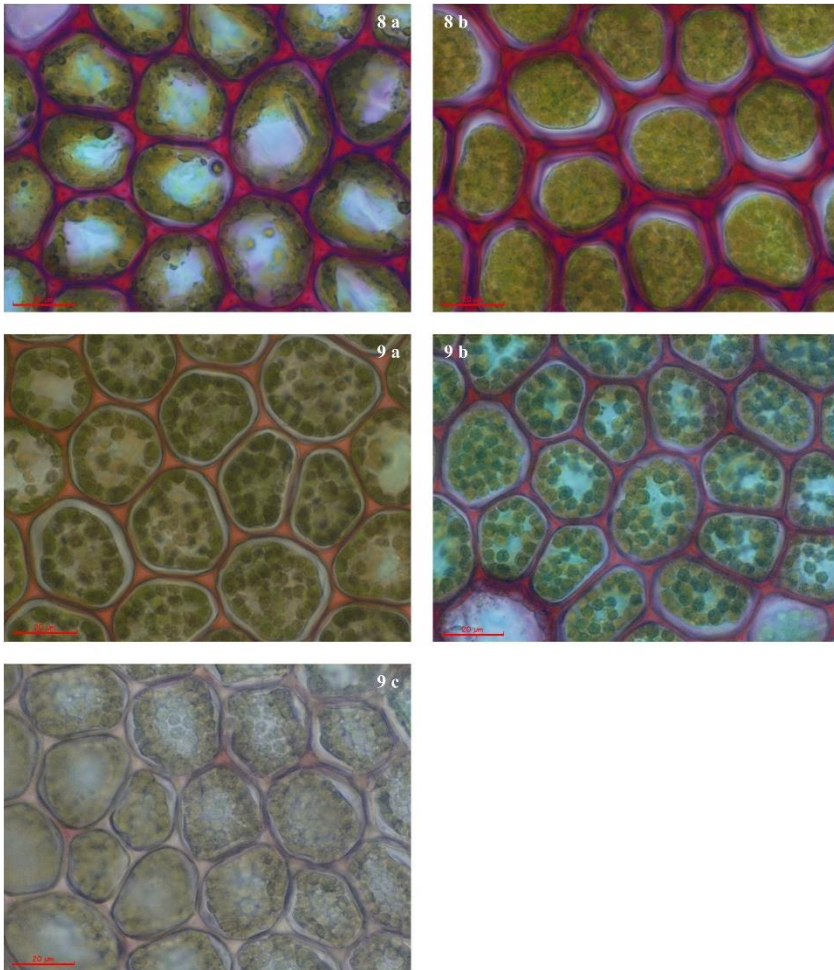


Photo 8a, b. *P. platyphylla* leaf cells at full turgor were frozen at a) -18°C and b) -80°C . After freezing neutral red staining was applied at pH 7.6. Scale bars = $2\ \mu\text{m}$.
Photo 9a, b, c. *P. platyphylla* leaf cells at full turgor were heated at a) 40°C and b) 50°C and c) 100°C for 5 minutes. Before heating treatments neutral red staining was applied at pH 7.6. Scale bars = $2\ \mu\text{m}$.

Heat treatment

Three high-temperature treatments (40 , 50 and 100°C) were applied for 5 and 10 minutes. During the 10-minute length period of the treatments at 40 or 50°C , the damage suffered by plant cells was not significantly distinguishable. Heating the *Porella* leaves at 100°C for 5 or 10 minutes did not result in distinct effect either.

Comparing the unstained and the neutral red stained samples of the cells it was found that the use of neutral red had a moderate protective role against high temperature. After applying the 40°C as heat treatment oil bodies were not visible, the chloroplasts were deformed in both the stain-free and the coloured samples. The tonoplasts were injured and the neutral red trapped in the vacuoles until then was released, became charged and the neutral red cations stained the cell walls. In the coloured cells – compared with the unstained ones – a slight rate of plasmolysis was noticed, but the basic cell structure remained unchanged (*Photo 9a*).

After applying the 50°C as heat treatment chloroplasts were strongly damaged and deformed, but their original arrangement remained unchanged, maybe due to the effect of the heat on the cytoskeleton. The plasmolysis was more emphasized than in the 40°C-treated cells (*Photo 9b*). After the 100°C treatment, the stain was released from the cells, but the cells remained relatively intact. The chloroplasts were deformed and their internal structure was eliminated (*Photo 9c*).

Monitoring the regeneration of *P. platyphylla* leaf cells after 5-month cold, subsequent 1-day desiccation and rewetting

After a 5-month cold in the dark (at 5°C), *P. platyphylla* leaves were desiccated for 1 day. 0, 10, 30, 40 minutes, 1, 24, and 48 hours after rehydration the regeneration of the cell structure was monitored by light microscopy. During the regeneration process a kind of trend could be observed. After 30 minutes, in the initial rewetting phase the cells were plasmolyzed softly and oil bodies started to be flattened (*Photo 10a*). 24 hours after the rewetting chloroplasts had a round shape instead of elliptical, oil bodies had a calyx form instead of a spindle shape (*Photo 10b*). 48 hours after rehydration chloroplasts completed their regeneration, oil bodies were seen as spectacularly big, shiny spherical organelles (*Photo 10b*).

24 hours after the rewetting is a critical point in the regeneration. Presumably, if the constitutive and inductive protection mechanisms are properly coordinated, the cell structure is capable of complete regeneration after the still tolerable stress effect they suffered, as can be seen by light microscopy.

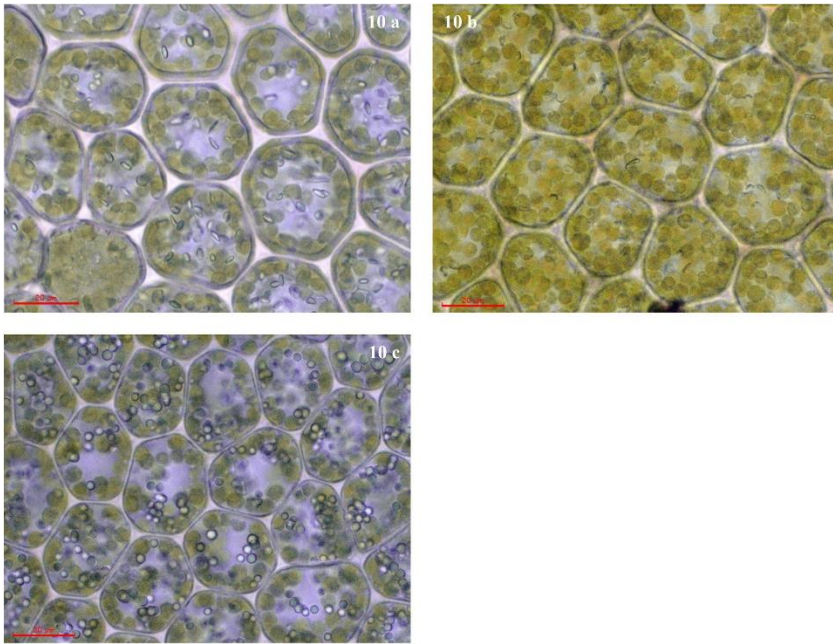


Photo 10a, b, c. Monitoring the regeneration of *P. platyphylla* leaf cells after 5-month cold, subsequent 1-day drying and rewetting. The leaf cells of *P. platyphylla* following rehydration after a) 30 min, b) 24 hours, c) 48 hours. Scale bars = 2 µm.

Osmotic stress applied by KSCN- and PEG-treatments

The 1 M KSCN-treatment (which represented a -4.38 MPa-strength osmotic stress to the cells) resulted in the most drastic effect in the shortest time. The cells began to be damaged after 10 minutes. The central vacuoles fragmented into smaller ones and then they disintegrated (*Photo 11a, b, 12a, b*). At the same time an irreversible destruction of chloroplasts began. The oil bodies started to become damaged only 1 hour after the treatment. So, the oil bodies proved to be the most resistant organelle against various stress factors. 0.5 M NaCl-treatment due to its -2.32 MPa-strength osmotic stress effect had the same influence on the cell structure as 1 M KSCN did, but after 40 minutes.

The 25% PEG does not penetrate into the cells, only develop higher osmotic pressure in the intercellular space. The osmotic effect of the 25% PEG developed later than the effect of the 1 M KSCN, due to the milder osmotic effect of the 25% PEG (-1.435 MPa), but the process of the plasmolysis was similar, the oil bodies

remained intact the longest and the vacuole membrane was damaged first in the two-hundredth minute (*Photo 13a, b*). The 25% PEG resulted in its maximal effect, total plasmolysis, in *Allium cepa* leaves within 5 minutes.

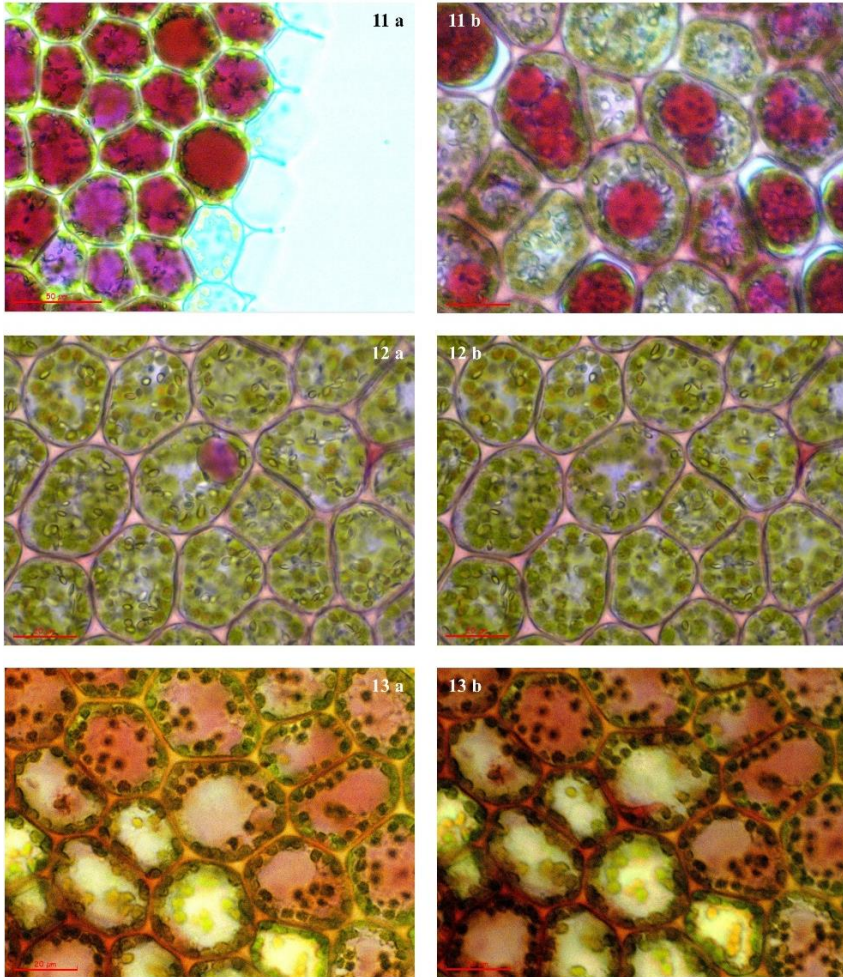


Photo 11a, b. The effect of 1 M KSCN-treatment after a) 0 minute, b) 10 minutes on the fully turgid leaf cells of *P. platyphylla* stained with neutral red at pH 7.6. Scale bars = 2 μ m. **Photo 12a, b.** The effect of 1 M KSCN-treatment after a) 11 minutes, b) 12 minutes on the fully turgid leaf cells of *P. platyphylla* stained with neutral red at pH 7.6. Scale bars = 2 μ m. **Photo 13a, b.** The effect of 25% PEG-treatment after a) 200 minutes, b) 201 minutes on the fully turgid leaf cells of *P. platyphylla* stained with neutral red at pH 7.6. Scale bars = 2 μ m.

CONCLUSIONS

The leaf cells of the extremely desiccation tolerant leafy liverwort, *P. platyphylla* contain lots of oval chloroplasts and shiny homogeneous oil bodies are visible in turgid cells. Oil bodies in *P. platyphylla* are small, massula type, homogenous, simple, round, 1-2 μm size, numerous, and not very distinct. Like many other DT liverworts, *P. platyphylla* is extremely difficult to infiltrate with resin (Duckett *et al.* 1988), the improminent oil bodies do not fix and embed well for electron microscopy (Duckett *et al.* 2006a, 2006b). The leaf cells of this liverwort due to their one-cell layered structure can be studied natively by light microscope. In the lack of a good electron microscopic embedding technique, views we get by light microscopy from this liverwort could be important and valuable.

We monitored the effects of various abiotic stress factors at cell level following the rate of plasmolysis, and the changes in the structure of cell organelles (chloroplasts, vacuoles, oil bodies). Furthermore our aim was to test the applicability of different stains (neutral red, toluidine blue, methylene blue, Sudan-III) in *Porella platyphylla* cells under experimental treatments. Natural drying at room temperature (for 1 day, 1 week, '62 years' by checking an old herbarium sample), subsequent rehydration, freezing at -18 and -80°C, heat treatment at 40, 50 and 100°C (for 5 and 10 min), osmotic and salt stress (0.5 M NaCl, 1 M KSCN, 25% PEG8000) were applied. In the course of monitoring the various stress factors the use of neutral red (at pH 7.6) staining proved to be the most optimal. In control plants one big cherry coloured vacuole could be discovered after staining. The central vacuole fragmented into small pieces, then ruptured after 10 minutes due to the strongest osmotic treatment (1 M KSCN). At the same time chloroplasts were irreversibly disrupted. The oil bodies proved to be the most resistant structures against the various stress factors. The freezing at -18°C resulted in more visible damage symptoms in the cell structure than freezing at -80°C. In the 62-year-old herbarium tissue it was easy to monitor the desiccation effect as the whole membrane structure was damaged.

Plants hardened for 5-month long cold were able to regenerate their cell structure and metabolism within 48 hours after 1-day natural desiccation. During the regeneration process the following cell structural changes could be observed after 30 minutes, in the initial rewetting phase the cells were plasmolyzed softly and oil

bodies started to be flattened (*Photo 11a*). 24 hours after the rewetting chloroplasts had a round shape instead of elliptical, oil bodies has a calyx form instead of a spindle shape (*Photo 11b*). 48 hours after rehydration chloroplasts completed their regeneration, oil bodies were seen as spectacularly big, shiny spherical organelles.

The 24 hours after the rewetting is found to be a critical point in the regeneration process. Presumably, if the constitutive and inductive protection mechanisms are properly coordinated, the cell structure is capable of complete regeneration after the still tolerable stress effect they suffered, as can be seen by light microscopy.

The 3 different high temperature treatments (40, 50, 100°C) resulted in similar changes in the cell structure to those affected by the two freezing treatments. Tissues were coloured by neutral red before freezing and heat treatments suffered less injury compared with the unstained ones. Light microscopic studies are convenient to monitor the regeneration of the cell structure after stress. Our findings are in line with other authors' work concerning other liverwort species in that the oil bodies, while retaining their original volume during drying, collapse during rehydration (Pressel *et al.* 2009). Marschall *et al.* (1998) and this work also suggest a shifting of soluble carbohydrates or other moieties into the cytosol and provides more experimental evidence that the oil bodies may have a crucial role in desiccation tolerance. Major subcellular changes in mosses, *Selaginella lepidophylla* (Platt *et al.* 1994), and some DT angiosperms (Dalla Vecchia *et al.* 1998; Navari-Izzo *et al.* 2000) include fragmentation of the vacuole and rounding of the chloroplasts (Li *et al.* 2014) and mitochondria, with the thylakoids and cristae remaining undamaged during the regeneration after desiccation or osmotic stress. The cell structure and its changes in the *P. platyphylla* during the various stress experiments give a good explanation of the stress tolerance of the species under natural circumstances.

Acknowledgement – The authors are grateful to Albert Vermes for reading and correcting the English language of the manuscript and also for the financial support of the EMMI 2015/16 researcher fellowship.

REFERENCES

ASAKAWA, Y. (1995). *Chemical constituents of the bryophytes. Progress in the chemistry of organic natural products*. Vol 65. Springer, Vienna. 615 pp.

- CHALAUD, G. (1931). Germination des spores et formation du gametophyte chez *Lophocolea cuspidata* et *Chiloscyphus polyanthus*. *Annales of Bryology* **4**: 49–78.
- DALLA VECCHIA, F., ASMAR, T.E., CALAMASSI, R., RASCIO, N. & VAZZANA, C. (1998). Morphological and ultrastructural aspects of dehydration and rehydration in leaves of *Sporobolus stapfianus*. *Plant Growth Regulation* **24**(3): 219–228.
- DUCKETT, J.G. (1986). Ultrastructure in bryophyte systematics and evolution: an evaluation. *Journal of Bryology* **14**: 25–42.
- DUCKETT, J.G., CARAFA, A. & LIGRONE, R. (2006a). A highly differentiated glomeromycotean association with the mucilage-secreting, primitive antipodean liverwort *Treubia* (Treubiaceae): clues to the origins of mycorrhizas. *American Journal of Botany* **93**(6): 797–813.
- DUCKETT, J.G. & CLYMO, R.S. (1988). Regeneration of bog liverworts. *New Phytologist* **110**(1): 119–127.
- DUCKETT, J.G. & LIGRONE, R. (1995). The formation of catenate foliar gemmae and the origin of oil bodies in the liverwort *Odontoschisma denudatum* (Mart.) Dum. (Jungermanniales): a light and electron microscope study. *Annals of Botany* **76**: 405–419.
- DUCKETT, J.G., RUSSEL, J. & LIGRONE, R. (2006b). Basidiomycetous endophytes in jungermannialean (leafy) liverworts have novel cytology and species-specific host ranges: a cytological and experimental study. *Canadian Journal of Botany* **84**(7): 1075–1093.
- GALATIS, B., APOSTOLAKOS, P. & KATSAROS, C. (1978). Ultrastructural studies on the oil bodies of *Marchantia paleacea* Bert. I. Early stages of oil-body cell differentiation: origination of the oil body. *Canadian Journal of Botany* **56**: 2268–2285.
- GAVAUDAN, P. (1927). Sur l'origine et les caractères des éléments olifères des Jungermanniales. *C.R. Acad. Sci.* **184**: 1473–1475.
- HE, X., SUN, Y. & ZHU, R. (2013). The Oil Bodies of Liverworts: Unique and Important Organelles in Land Plants. *Critical Reviews in Plant Sciences* **32**: 293–302.
- HE-NYGRÉN, X., JUSLÉN, A., AHONEN, I., GLENNY, D. & PIIPPO, S. (2004). Phylogeny of liverworts – beyond a leaf and a thallus. *Monographs in Systematic Botany from the Missouri Botanical Garden* **98**: 87–118.
- HIERONYMUS, G. (1892). Beiträge zur Morphologie und Biologie der Algen. *Beiträge zur Biologie der Pflanzen* **5**: 461–495.
- KENRICK, P. & CRANE, P.R. (1997). The origin and early evolution of land plants. *Nature* **389**: 33–39.
- KIS, G. & PÓCS, T. (1997). Oil body studies on African Hepaticae. *Journal of the Hattori Botanical Laboratory* **81**: 175–242.
- LI, J., LI, X. & CHEN, C. (2014). Degradation and reorganization of thylakoid protein complexes of *Bryum argenteum* in response to dehydration and rehydration. *The Bryologist* **117**(2): 110–118.
- MARSCHALL, M., PROCTOR, M.C.F. & SMIRNOFF, N. (1998). Carbohydrate composition and invertase activity of the leafy liverwort *Porella platyphylla*. *New Phytologist* **138**: 343–353.
- MARSCHALL, M. & PROCTOR, M.C.F. (1999). Desiccation tolerance and recovery of the leafy liverwort *Porella platyphylla* (L.) Pfeiff.: chlorophyll-fluorescence measurements. *Journal of Bryology* **21**: 257–262.

- MÜLLER, K. (1906). *Die Lebermoose*. Pages 65-128 in: Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich, und der Schweiz. 2nd ed. Vol 6. Leipzig, E. Kummer.
- NAVARI-IZZO, F., QUARTACCI, M.F., PINZINO, C., RASCIO, N., VAZZANA, C. & SGHERRI, C.L.M. (2000). Protein Dynamics in Thylakoids of the Desiccation-Tolerant Plant *Boea hygroskopica* during Dehydration and Rehydration. *Plant Physiology* **124**(3):1427–1436.
- PATON, J.A. (1999). *The liverwort flora of the British Isles*. Harley, Colchester, England, 626 pp.
- PLATT, K.A., OLIVER, M.J. & THOMSON, W.W. (1994). Membranes and organelles of dehydrated *Selaginella* and *Tortula* retain their normal configuration and structural integrity: freeze fracture evidence. *Protoplasma* **178**(1): 57–65.
- PRESSEL, S., DUCKETT, J.G., LIGRONE, R. & PROCTOR, M.C.F. (2009). Effects of de- and rehydration in desiccation-tolerant liverworts: A cytological and physiological study. *International Journal of Plant Sciences* **170**(2): 182–199.
- PRESSEL, S., LIGRONE & DUCKETT, J. G. (2006). Effects of de-and rehydration on food-conducting cells in the moss *Polytrichum formosum*. Hedw.: a cytological study. *Annals of Botany* **98**: 67–76.
- PROCTOR, M.C.F., LIGRONE, L. & DUCKETT, J. G. 2007(a). Desiccation tolerance in the moss *Polytrichum formosum*: physiological and fine-structural changes during desiccation and recovery. *Annals of Botany* **99**: 75–93.
- PROCTOR, M.C.F., OLIVER, M.J., WOOD, A.J., ALPERT, P., STARK, L.R., CLEAVITT, N.L. & MISHLER, B.D. 2007(b). Desiccation-tolerance in bryophytes: a review. *The Bryologist* **110**(4): 595–621.
- QUI, Y.L., LI, L., WANG, B., CHEN, Z., KNOOP, V., GROTH-MALONEK, M., DOMBROVSKA, O., LEE, J., KENT, L., REST, J., ESTABROOK, G.F., HENDRY, T.A., TAYLOR, D.W., TESTA, C.M., AMBROS, M., CRANDALL-STOTLER, B., DUFF, R.J., STECH, M., FREY, W., QUANDT, D. & DAVIS C.C. (2006). The deepest divergence in land plants inferred from phylogenetic evidence. *PNAS* **17**: 15511–15516.
- RUBINSTEIN, C.V., GERRIENNE, P., DE LA PUENTE, G.S., ASTINI, R.A. & STEEMANS, P. (2010). Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist* **188**: 365–369.
- SASS-GYARMATI, A. (2015). Taxonomical revision of *Lopholejeunea* (Spruce) Schiffn. (Lejeuneaceae, Hepaticae) in Africa (in Hungarian). PhD Dissertation, Szent István University, Gödöllő, 109 pp.
- SMIRNOFF, N. (1992). The carbohydrates of bryophytes in relation to desiccation tolerance. *Journal of Bryology* **17**: 185–191.
- STEWART, G.H. (1978). Oil bodies of the New Zealand leafy Hepaticae (Jungermanniales). *New Zealand Journal of Botany* **16**: 185–205.
- SUIRE, C. (1975). Les données actuelles sur la chimie des Bryophytes. *Review of Bryology and Lichenology* **41**: 105–256.
- SUIRE, C., BOUVIER, F., BACKHAUS, R.A., BÉGU, D., BONNEU, M. & CAMARA, B. (2000). Cellular localization of isoprenoid biosynthetic enzymes in *Marchantia polymorpha*. Uncovering a new role of oil bodies. *Plant Physiology* **124**: 971–978.
- WELLMAN, C.H., OSTERLOFF, P.L. & MOHLUDDIN, U. (2003). Fragments of the earliest land plants. *Nature* **425**: 282–284.

(submitted: 09.08.2016, accepted: 22.10.2016)

BRYOFLORESTICAL DATA FROM AUSTRIAN PART OF SOPRON HILLS (ÖDENBURGER-GEBIRGE, E-AUSTRIA)

Péter Szűcs^{1*} & *Harald Zechmeister*²

¹*Eszterházy Károly University, Institute of Biology, Department of Botany and Plant Physiology, H-3300 Eger, Leányka u. 6, Hungary;*

²*University of Vienna, Department of Botany and Biodiversity Research, Rennweg 14, 1030 Wien, Austria; *E-mail: szucs.peter@uni-eszterhazy.hu*

Abstract: The Austrian part of Sopron Hills was a neglected area from the point of view of bryophyte floristics. In the investigated area 141 bryophytes were found, out of these 21 liverworts and 120 mosses. There were nine species new to Burgenland: *Jungermannia gracillima*, *Pellia neesiana*, *Campylopus pyriformis*, *Leucobryum juniperoideum*, *Orthotrichum lyellii*, *Pohlia elongata*, *Pohlia prolifera*, *Pseudephemerum nitidum*, *Trichodon cylindricus*.

Some species were detected from the territory which are otherwise rare in Austria, such as: *Fossombronia wondraczekii*, *Riccardia palmata*, *Brachythecium mildeanum*, *Didymodon cordatus*, *Didymodon vinealis*, *Fissidens adianthoides*, *Microbryum davallianum*, *Plagiomnium elatum*, *Pleuridium acuminatum*, *Pleuridium subulatum*, *Pottia intermedia*, *Pseudephemerum nitidum*.

13 species are listed as threatened in the Red Data List of bryophytes in Lower Austria, and so do 11 species in the overall Austrian Red Data list of bryophytes. No species of the Annex II of the FFH-directive were found.

Keywords: bryophytes, rare species, red-list status, Burgenland

INTRODUCTION

To date no significant bryological research has been carried out at the Austrian part of the Sopron Hills, leaving this territory almost unexplored. The overall Burgenland itself has only a very marginal recent bryological examination. The research of Latzel (1941) involved only the Hungarian parts of the Lower Alps. The work of Maurer (1965) on the moss species of the Burgenland presents field data for the Southern part of the Burgenland. Schlüsslmayr (2001) examined the Leithagebirge in northern Burgenland and Zechmeister (2004, 2005a) studied the bryophyte flora of the

Seewinkel. Another research of Zechmeister (2008) involved the peatmoss habitats of the Burgenland. Within the region of these studies only the work of Zechmeister (2005b) describes the serpentine outcrops in the area. Preliminary results for the Sopron Hills have first been published by Szűcs and Szmorad (2009). No checklist or Red Data List can be found for the Burgenland. The Red Data List of Lower Austria, which was based on abundant latest floristical data, has been published only recently (Zechmeister *et al.* 2013). Nevertheless, the Sopron Hills are located beyond the boundaries of the Lower Austria region, which makes the relation and direct comparison of the obtained data difficult.

The proposed article intends to fill this gap in knowledge and provides the latest bryofloristical results for the Sopron Hills.

Study area

The Sopron Hills are the north-eastern and relatively low height (between 600 and 800 m a.s.l.) subrange of the Alps. To the west they are separated from the adjacent, nearly north-south running Rosalia Hills by a saddle above the village of Siegraben (Szmorad 2011).

In aspect of geology the western part of the hills towards the Rosalia Hills is covered with miocene sandy, gravel–clay sediments. In the southern part of the hills (between Ritzing and Neckenmarkt, also south of Kalkgruben) there are penetrations of Leitha limestone, and acidic sandstones located between Neckenmarkt and Harka. In the north-western part of the region, large-scale areas are covered with a Badenian clay formation (Szmorad 2011). The most frequent soil types of the territory are brown forest soils. The hydrographic network of the area consists of small streams. The eastern hill front is warmer and dryer, the western, inner area is much cooler and has higher precipitation. The mean annual temperature varies between 8–9 °C, and the annual precipitation usually between 650–900 mm (Király 2004, Szmorad 2011).

From the phytogeographical point of view the Sopron Hills are situated in the border region of the Eastern Alpine (*Noricum*) and the Pannonian (*Pannonicum*) floristic regions. In the hills the mesophilous and acidophilous deciduous forests are dominant, but there are large-scale areas of secondary coniferous forest stands (Király 2004, Szmorad 2010).

MATERIALS AND METHODS

The fieldwork has been carried out between 2009 and 2014. The main habitats, such as acidophyllous deciduous and mixed forests, planted coniferous forests, wetlands, grasslands, streams, forest roads, lakes, quarries and buildings were investigated based on a subjective site selection. Bryophytes were collected from all available substrates (soil, concrete, tree bark and root, decayed wood, stone and plastic foil).

The nomenclature follows Köckinger *et al.* (2015). The species names are given, as well as the Red Data List status which was given to these species for Lower Austria by Zechmeister *et al.* (2013), number of sampling site(s) and the substrate within. Specimens have been deposited in bryophyte collections of the Eszterházy Károly University in Eger (EGR) and in the private herbarium of Harald Zechmeister at University of Vienna. The site details are listed in the appendix.

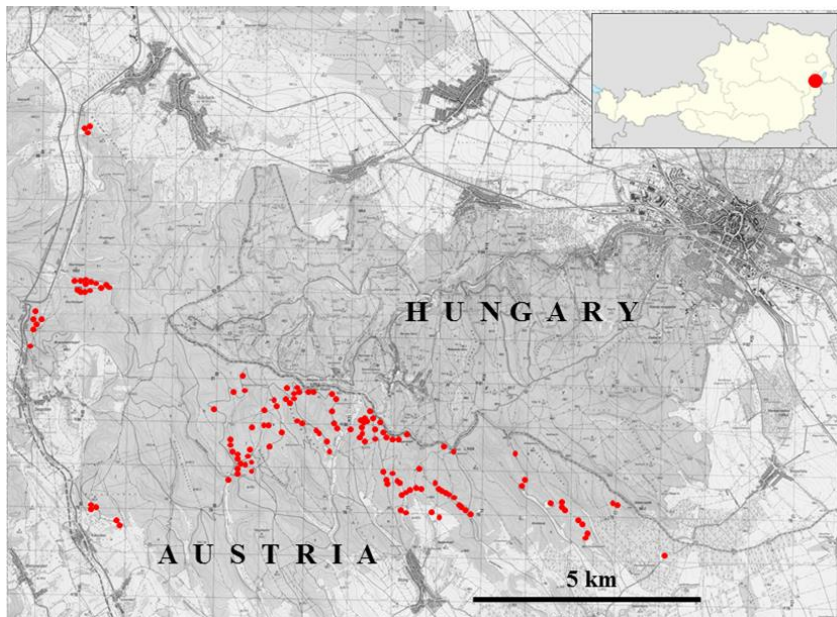


Figure 1. The sampling sites in the investigated area

RESULTS

List of species

In total 141 species were found, out of these were 120 bryophytes and 21 liverworts.

Hepaticeae

Blasia pusilla L. – LC – 79, 80: on soil

Calypogeia fissa (L.) Raddi – LC – 101: on soil

Cephalozia bicuspidata (L.) Dumort. – LC – 98, 101: on soil

Cephaloziella divaricata (Sm.) Schiffn. – LC – 7, 38, 62, 66, 63, 90: on soil

Conocephalum conicum (L.) Dumort. – LC – 46: on soil

Fossombronia wondraczekii (Corda) Lindb. – NT – 79: on soil

Frullania dilatata (L.) Dumort. – LC – 13: bark of *Fagus sylvatica*; 86: bark of *Malus sylvestris*

Jungermannia gracillima Sm. – LC – 63, 66: on soil

Lophocolea bidentata (L.) Dumort. – LC – 75, 67, 84: on soil

Lophocolea heterophylla (Schrad.) Dumort. – LC – 14: root of *Alnus glutinosa*; 16: on bark; 15, 78: on decayed wood; 90: on soil; 108: on rooted *Picea abies* trunk

Lophocolea minor Nees – LC – 33: on soil

Metzgeria furcata (L.) Dumort. – LC – 108: on bark of *Tilia*; 119: on bark of *Fagus sylvatica*

Nowellia curvifolia (Dicks.) Mitt. – LC – 108: on rooted *Picea abies* trunk

Pellia endiviifolia (Dicks.) Dumort. – LC – 4, 79: on soil

Pellia neesiana (Gottsche) Limpr. – LC – 30: on soil

Plagiochila asplenoides (L. emend. Taylor) Dumort. – LC – 46, 108: on soil

Plagiochila porelloides (Torr. ex Nees) Lindenb. – LC – 70, 84: on soil

Ptilidium pulcherrimum (Weber) Vain. – LC – 90: on soil; 91: bark of *Quercus petraea*

Radula complanata (L.) Dumort. – LC – 19: bark of *Acer campestre*; 46: bark of *Acer pseudoplatanus* and *Alnus glutinosa*; 78: bark of *Corylus avellana*; 119: bark of *Fagus sylvatica*

Riccardia palmata (Hedw.) Carruth. – VU – 108: on rooted *Picea abies* trunk

Scapania nemorea (L.) Grolle – LC – 101: on soil

Musci

- Abietinella abietina*** (L. ex Hedw.) M.Fleisch. var. ***abietina*** – LC – 87: on soil
- Amblystegium riparium*** (L. ex Hedw.) Schimp. – LC – 16: on bark and root; 77: on piece of wood
- Amblystegium serpens*** (L. ex Hedw.) Schimp. – LC – 19: bark of *Acer campestre*; 21, 71: on concrete; 74: bark of *Alnus glutinosa*, bark of *Sambucus nigra*; 78: bark of *Corylus avellana*
- Anomodon attenuatus*** (Hedw.) Huebener – LC – 116: on limestone
- Anomodon viticulosus*** (Hedw.) Hook. & Taylor – LC – 116: on limestone
- Atrichum undulatum*** (Hedw.) P.Beauv. – LC – 2, 3, 8, 10, 12, 14, 62, 63, 90: on soil
- Barbula convoluta*** Hedw. – LC – 5: on soil
- Barbula unguiculata*** Hedw. – LC – 44, 77, 89: on soil
- Bartramia pomiformis*** Hedw. – LC – 108: on soil
- Brachytheciastrum velutinum*** (L. ex Hedw.) Ignatov & Huttunen – LC – 1, 14, 16: on decayed wood and soil; 7, 33, 46: on soil; 74: bark of *Alnus glutinosa*
- Brachythecium albicans*** (Neck. ex Hedw.) Schimp. – LC – 39, 42, 87: on soil
- Brachythecium glaerosum*** (Bruch ex Spruce) Schimp. var. ***glareosum*** – LC – 3, 10, 11, 87: on soil
- Brachythecium mildeanum*** (Schimp.) Schimp. – EN – 109: on soil
- Brachythecium rivulare*** Schimp. – LC – 16: on root; 50: stump of *Alnus glutinosa*; 75, 76, 89: on soil; 78, 106: on decayed wood
- Brachythecium rutabulum*** (L. ex Hedw.) Schimp. – LC – 16: on bark; 78: on decayed trunk, on concrete; 4, 39, 42, 77: on soil; 83: on decayed wood
- Brachythecium salebrosum*** (Hoffm. ex F.Weber & D.Mohr) Schimp. – LC – 7: on soil; 14, 74: bark of *Alnus glutinosa*, bark of *Sambucus nigra*
- Bryum argenteum*** Hedw. – LC – 116: on soil
- Bryum capillare*** Hedw. – LC – 104: on soil
- Bryum elegans*** Nees var. ***elegans*** – LC – 73: on soil
- Bryum moravicum*** Podp. – LC – 47: bark of *Fraxinus* sp.; 119: bark of *Fagus sylvatica*
- Bryum rubens*** Mitt. – LC – 62: on soil

- Callierygonella cuspidata*** (L. ex Hedw.) Loeske – LC – 3, 20, 55, 56, 63, 75: on soil; 71: on plastic foil; 78: on concrete, on decayed wood
- Campylopus pyriformis*** (Schultz) Brid. – VU – 53: on soil
- Ceratodon purpureus*** (Hedw.) Brid. – LC – 2, 6, 7, 10, 11, 13, 39, 42, 48, 60, 62, 87, 90: on soil
- Cirriphyllum crassinervium*** (Taylor) Loeske & M.Fleisch. – LC – 116: on limestone
- Cirriphyllum piliferum*** (Schreb. ex Hedw.) Grout – LC – 18, 39, 42, 48, 63, 77: on soil
- Climacium dendroides*** (Hedw.) F.Weber & D.Mohr – LC – 18: on soil
- Cratoneuron filicinum*** (L. ex Hedw.) Spruce – LC – 37, 50, 56, 77, 78: on soil
- Dicranella heteromalla*** (Hedw.) Schimp. – LC – 2, 7, 10, 12, 13, 62, 63, 68, 79, 90: on soil
- Dicranella staphylina*** H.Whitehouse – LC – 39: on soil
- Dicranella varia*** (Hedw.) Schimp. – LC – 77: on soil
- Dicranum montanum*** Hedw. – LC – 10, 12, 15: on decayed wood; 81: on decayed log; 91: bark of *Quercus petraea*; 91: on soil
- Dicranum polysetum*** Sw. ex anon. – LC – 62: on soil
- Dicranum scoparium*** Hedw. – LC – 6: on decayed wood; 13, 38, 42, 90, 91: on soil; 82: stump of *Alnus glutinosa*
- Didymodon cordatus*** Jur. – NT – 111: on soil; 115: surface of calcareous building; 116: on limestone
- Didymodon rigidulus*** Hedw. – LC – 115: surface of calcareous building; 116: on limestone
- Didymodon vinealis*** (Brid.) R.H.Zander – EN – 115: surface of calcareous building
- Drepanocladus aduncus*** (Hedw.) Warnst. – LC – 77: on soil
- Encalypta streptocarpa*** Hedw. – LC – 116: on limestone
- Eurhynchiastrum pulchellum*** (Hedw.) Ignatov & Huttunen var. ***pulchellum*** – LC – 70: on soil
- Eurhynchium angustirete*** (Broth.) T.J.Kop. – LC – 14: decayed wood; 39, 42, 63, 67, 68, 73, 84, 91: on soil
- Fissidens adianthoides*** Hedw. – NT – 57: on soil
- Fissidens bryoides*** Hedw. – LC – 73: on soil
- Fissidens taxifolius*** Hedw. subsp. ***taxifolius*** – LC – 1: on soil
- Funaria hygromertica*** Hedw. – LC – 62, 120: on soil
- Grimmia pulvinata*** (Timm. ex Hedw.) Sm. – LC – 71: on concrete
- Herzogiella seligeri*** (Brid.) Z.Iwats. – LC – 6, 15: on decayed wood

- Heterocladium heteropterum*** (Brid.) Schimp. – LC – 43: on soil
Homalia trichomanoides (Hedw.) Brid. – LC – 49: on root
Homalothecium lutescens (Hedw.) H.Rob. – LC – 3: on soil
Homalothecium philippeanum (Spruce) Schimp. – LC – 47: bark of
Fraxinus sp.; 116: on limestone
Homomallium incurvatum (Schrad. ex Brid.) Loeske – LC – 21: on
concrete; 116: on limestone
Hylocomnium splendens (Hedw.) Schimp. – LC – 18, 91: on soil
Hypnum cupressiforme Hedw. var. ***cupressiforme*** – LC – 1: on
decayed wood and soil; 14: root of *Alnus glutinosa*; 47: bark of
Fraxinus; 78: bark of *Alnus glutinosa*; 8, 38, 84, 90, 91: on soil; 90:
bark of *Malus sylvestris*
Hypnum cupressiforme var. ***lacunosum*** Brid. – LC – 73: on soil
Hypnum lindbergii Mitt. – LC – 71: on plastic foil; 78: on decayed
wood, 4, 39, 48, 84: on soil
Isothecium alopecuroides (Lam. ex Dubois) Isov. – LC – 119: root
swelling of *Fagus sylvatica*
Leskea polycarpa Ehrh. ex Hedw. – LC – 19: bark of *Acer campestre*
Leucobryum glaucum (Hedw.) Ångstr. – LC – 91: on soil
Leucobryum juniperoideum (Brid.) Müll.Hal. – LC – 90, 91: on soil
Leucodon sciuroides (Hedw.) Schwägr. – LC – 86: bark of *Malus*
sylvestris
Microbryum davallianum (Sm.) R.H.Zander – EN – 44: on soil
Mnium hornum Hedw. – LC – 108: root swelling of *Tilia* sp.
Mnium marginatum (Dicks.) P.Beauv. – LC – 115: surface of
calcareous building
Orthotrichum affine Schrad. ex Brid. – LC – 28: bark of *Fraxinus* sp.
Orthotrichum anomalum Hedw. – LC – 21: on concrete; 116: on
limestone
Orthotrichum cupulatum Hoffm. ex Brid. var. ***cupulatum*** – LC –
116: on limestone
Orthotrichum diaphanum Schrad. ex Brid. – LC – 65: bark of
Sambucus nigra
Orthotrichum lyellii Hook. & Taylor – LC – 28: on bark of *Fraxinus*
sp.
Orthotrichum obtusifolium Brid. – LC – 25: on bark of *Fraxinus* sp.
Orthotrichum pallens Bruch ex Brid. – LC – 35: bark of *Fagus*
sylvatica
Orthotrichum speciosum Nees – LC – 35: bark of *Fagus sylvatica*

- Oxyrrhynchium hians* (Hedw.) Loeske var. ***hians*** – LC – 82: root swelling of *Alnus glutinosa*; 89: on soil
- Palustriella commutata* (Hedw.) Ochyra var. ***commutata*** – LC – 57, 109: on soil; 71: on plastic foil
- Phascum cuspidatum* Schreb. ex Hedw. var. ***cuspidatum*** – LC – 44, 45: on soil
- Physcomitrium pyriforme* (Hedw.) Bruch & Schimp. – LC – 60: on soil
- Plagiomnium affine* (Blandow ex Funck) T.J.Kop. – LC – 78: on decayed trunk; 18, 73, 90: on soil
- Plagiomnium cuspidatum* (Hedw.) T.J.Kop. – LC – 16: on root; 18: on soil; 78: on concrete
- Plagiomnium elatum* (Bruch & Schimp.) T.J.Kop. – VU – 68: on soil
- Plagiomnium rostratum* (Schrad.) T.J.Kop. – LC – 106: on decayed wood
- Plagiomnium undulatum* (Hedw.) T.J.Kop. – LC – 21, 68, 75, 78: on soil; 15: on decayed wood; 82: stump of *Alnus glutinosa*
- Plagiothecium cavifolium* (Brid.) Z.Iwats. – LC – 12, 63: on soil
- Plagiothecium denticulatum* (L. ex Hedw.) Schimp. – LC – 12: on soil; 15: on decayed wood
- Plagiothecium laetum* Schimp. var. ***laetum*** – LC – 12, 13, 16: on soil
- Plagiothecium nemorale* (Mitt.) A.Jaeger – LC – 12: on soil
- Plagiothecium succulentum* (Wilson) Lindb. – LC – 16, 63: on soil
- Platygyrium repens* (Brid.) Schimp. – LC – 78: bark of *Alnus glutinosa*
- Pleuridium acuminatum* Lindb. – VU – 2, 62: on soil
- Pleuridium subulatum* (Hedw.) Rabenh. – NT – 5, 63: on soil
- Pleurozium schreberi* (Willd. ex Brid.) Mitt. – LC – 18, 39, 42, 62, 84: on soil
- Pogonatum aloides* (Hedw.) P.Beauv. – LC – 62, 63: on soil
- Pohlia elongata* Hedw. var. ***elongata*** – LC – 12: on soil
- Pohlia melanodon* (Brid.) A.J.Shaw – LC – 1, 89: on soil
- Pohlia nutans* (Hedw.) Lindb. subsp. ***nutans*** – LC – 2, 6, 63, 90: on soil
- Pohlia prolifera* (Kindb.) Lindb. ex Broth. – VU-R – 54: on soil
- Pohlia wahlenbergii* (F.Weber & D.Mohr) A.L.Andrews var. ***wahlenbergii*** – LC – 5: on soil
- Polytrichum formosum* Hedw. – LC – 2, 6, 11, 13, 90: on soil
- Polytrichum juniperinum* Willd. ex Hedw. – LC – 48, 79, 90: on soil

- Polytrichum piliferum*** Schreb. ex Hedw. – LC – 8, 62, 70, 90, 111: on soil
- Pottia intermedia*** (Turner) Fürnr. – VU – 39: on soil
- Pottia truncata*** (Hedw.) Bruch & Schimp. – LC – 35: on soil
- Pseudephemerum nitidum*** (Hedw.) Loeske – EN – 98: on soil
- Pseudeskeella nervosa*** (Brid.) Nyholm – LC – 19: bark of *Acer campestre*
- Pseudoscleropodium purum*** (L. ex Hedw.) M.Fleisch. – LC – 39, 42, 84, 90, 114: on soil
- Pterigynandrum filiforme*** Hedw. var. ***filiforme*** – LC – 119: on bark of *Fagus sylvatica*
- Pylaisia polyantha*** (Hedw.) Schimp. – LC – 19: bark of *Acer campestre*; 74: bark of *Sambucus nigra*; 78: bark of *Corylus avellana*
- Racomitrium canescens*** (Timm. ex Hedw.) Brid. subsp. ***canescens*** – LC – 89: on soil
- Rhizomnium punctatum*** (Hedw.) T.J.Kop. – LC – 16: on root and bark; 74: bark of *Alnus glutinosa*; 15, 83: on decayed wood; 46, 50, 82: stump of *Alnus glutinosa*
- Rhyncostegium murale*** ((Neck. ex Hedw.) Schimp. – LC – 21: on concrete; 115: on calcareous building
- Rhytidiadelphus squarrosus*** (L. ex Hedw.) Warnst. – LC – 18, 42, 84: on soil
- Schistidium crassipilum*** H.H.Blom – LC – 21, 71: on concrete
- Syntrichia ruralis*** (Hedw.) F.Weber & D.Mohr – LC – 86: on concrete
- Tetraphis pellucida*** Hedw. – LC – 16, 106, 113: on decayed wood
- Thuidium assimile*** (Mitt.) A.Jaeger – LC – 39: on soil; 78: on decayed wood
- Thuidium delicatulum*** (Hedw.) Schimp. – LC – 18, 38, 84: on soil
- Thuidium tamariscinum*** (Hedw.) Schimp. – LC – 18, 78: on decayed wood; 42, 68: on soil
- Trichodon cylindricus*** (Hedw.) Schimp. – LC – 1, 17: on soil
- Tortula muralis*** Hedw. var. ***muralis*** – LC – 71: on concrete
- Ulota bruchii*** Hornsch. ex Brid. – LC – 25, 110: bark of *Fraxinus* sp.
- Ulota crispa*** (Hedw.) Brid. – LC – 17: bark of *Betula pendula*

DISCUSSION

On the basis of these results, the bryophyte list of the project area was compared to the national (Grims and Köckinger 1999, Saukel and Köckinger 1999) and regional bryophyte Red Data List (Zechmeister *et al.* 2013) as well as to the Hungarian Red data List (Papp *et al.* 2010) (Table 1).

Table 1. The Red Data List status of bryophytes in Lower Austria (Niederösterreichs) (Zechmeister *et al.* 2013), Austria (Grims and Köckinger 1999, Saukel and Köckinger 1999) and Hungary (Papp *et al.* 2010).

Comments: Red Data List status in Austria: *VU (gefährdet), *reg. VU (r3 gefährdet), *EN (stark gefährdet) (Grims and Köckinger 1999, Saukel and Köckinger 1999).

Species name	Lower Austria	Austria	Hungary
<i>Blasia pusilla</i> (Hepaticaceae)	LC	LC	EN
<i>Calypogeia fissa</i>	LC	LC	NT
<i>Fossombronia wondraczekii</i>	NT	VU*	DD
<i>Jungermannia gracillima</i>	LC	LC	NT
<i>Nowellia curvifolia</i>	LC	LC	VU
<i>Pellia neesiana</i>	LC	LC	unknown
<i>Plagiochila asplenoides</i>	LC	LC	NT
<i>Ptilidium pulcherrimum</i>	LC	LC	NT
<i>Riccardia palmata</i>	VU	LC	NT
<i>Scapania nemorea</i>	LC	LC	VU
<i>Brachythecium mildeanum</i> (Musci)	EN	VU*	LC-att
<i>Brachythecium glaeosum</i> var. <i>glaeosum</i>	LC	LC	NT
<i>Campylopus pyriformis</i>	VU	EN*	DD
<i>Dicranella staphylina</i>	NT	LC	NT
<i>Didymodon cordatus</i>	NT	VU*	LC-att
<i>Didymodon vinealis</i>	EN	VU*	LC
<i>Eurhynchiastrum pulchellum</i> var. <i>pulchellum</i>	LC	LC	NT
<i>Fissidens adianthoides</i>	NT	reg. VU*	NT
<i>Heterocladium heteropterum</i>	LC	LC	unknown
<i>Microbryum davallianum</i>	EN	VU	LC-att
<i>Mnium hornum</i>	LC	LC	NT
<i>Orthotrichum cupulatum</i>	LC	reg. VU*	LC-att
<i>Orthotrichum obtusifolium</i>	LC	LC	NT
<i>Palustriella commutata</i> var. <i>commutata</i>	LC	LC	EN
<i>Plagiomnium elatum</i>	VU	VU	LC-att
<i>Plagiothecium succulentum</i>	LC	VU	LC
<i>Pleuridium acuminatum</i>	VU	LC	LC-att
<i>Pleuridium subulatum</i>	NT	LC	LC-att
<i>Pohlia elongata</i> var. <i>elongata</i>	LC	LC	DD
<i>Pohlia prolifera</i>	VU-R	LC	DD
<i>Pottia intermedia</i>	VU	LC	LC-att
<i>Pseudephemerum nitidum</i>	EN	VU	LC-att
<i>Ulota bruchii</i>	LC	LC	VU
<i>Ulota crispa</i>	LC	LC	NT

No species of the Annex II of the FFH-directive were found in the investigated area. However, *Leucobryum* sp. which is part of the Annex V of the respective directive was found several times (for details see the species list and corresponding site numbers).

The bryophyte flora of the investigated area resembles that of other lowlands in northern or southern Austria and despite its position in eastern Austria it has only a very small number of species typical or widespread in the Pannonian area (e.g. *Didymodon vinealis*). This is due to the fact that most habitats in the Sopron Hills do not represent typical eastern Austrian habitats as natural dry grasslands or vineyards. Furthermore, most of the sites are situated at comparable higher elevation as most of the sites in the east of Austria. In addition the investigated sites represent a wide range of woods and consequence microclimate and soils are more humid than at „typical” Pannonian sites.

Related to its bedrock the flora is dominated by acidophilous species and only a very few species related to calcareous bedrock were found. The large extent of woods in the area favours a wide range of shade tolerant plants, as well as epiphytes and species restricted to dead logs. Compared to other studies in the centre of the Pannonian area of the Burgenland (e.g. Zechmeister 2005b) which is slightly north of the study area, hepatics show a comparable high number in this study, which is mainly a result of the more humid situation in the investigated area.

The number of threatened species is low in our study as the investigated sites were situated within habitats which are neither threatened by human activity and none rare in occurrence, too.

Acknowledgement – The project was financed by the „Ernst Mach-Stipendium der AÖU der Aktion Österreich-Ungarn” and „Stipendium der AÖU für Universitätslehrer der Aktion Österreich-Ungarn” scholarships.

The article was funded by „Társadalmi Megújulás Operatív Program Kutatás, Innováció, Együttműködések – Társadalmi innováció és kutatási hálózatok együttműködésének erősítése az Eszterházy Károly Főiskola, a Bay Zoltán Alkalmazott Kutatási Nonprofit Kft. és az Agria TISZK Közhasznú Nonprofit Kft. együttműködésével” called project (TÁMOP-4.2.1.D-15/1/KONV-2015-0013). The project was supported by the European Union and the European Social Fund co-funded. The authors are grateful to Ferenc Szmorad and Tamás Pócs for their help in literature access and interpretation.

REFERENCES

- GRIMS, F. & KÖCKINGER, H. (1999). *Rote Liste gefährdeter Laubmoose (Musci) Österreichs*. In: NIKLFELD, H. (ed.), *Rote Liste gefährdeter Pflanzen Österreichs*. Austria Medien Service, Wien, pp. 157–171.
- KIRÁLY, G. (ed., 2004). A Soproni-hegység edényes flórája. (Die Gefäßpflanzenflora des Ödenburger Gebirges). *Flora Pannonica* 2(1): 7–12.
- KÖCKINGER, H., SCHRÖCK, C., KRISIAI, R. & ZECHMEISTER, H.G. (2015). Checklist of Austrian bryophytes. <http://131.130.59.133/projekte/moose/> [01.11.2015.]
- LATZEL, A. (1941). Beitrag zur Kenntnis der Moose des Ostralpenrandgebiets. *Beih. Bot. Centralbl.* 61: 211–260.
- MAURER, W. (1965). Die Moose des Südburgenlandes. *Wiss. Arb. Burgenland* 32: 5–40.
- PAPP, B., ERZBERGER, P., ÓDOR, P., HOCK, Zs., SZÖVÉNYI, P., SZURDOKI, E. & TÓTH, Z. (2010). Updated checklist and redlist of Hungarian bryophytes. *Studia botanica hungarica* 41: 31–59.
- SAUKEL, J. & KÖCKINGER, H. (1999). *Rote Liste gefährdeter Lebermoose (Hepaticae) und Hornmoose (Anthocerotae) Österreichs*. In: NIKLFELD, H. (ed.): *Rote Liste gefährdeter Pflanzen Österreichs*, Austria Medien Service, Wien, pp. 172–177.
- SCHLÜSSLMAYR, G. (2001). Die Moosvegetation des Leithagebirges im Burgenland. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 138: 65–93.
- SZMORAD, F. (2010). *A Soproni-hegység erdeinek történeti, növényföldrajzi és cönológiai vizsgálata*. (The historical, phytogeographical and coenological investigations on the forest of the Sopron Hills). PhD dissertation in manuscript, Pécsi Tudományegyetem Biológia Doktori Iskola, Pécs. 128 pp.
- SZMORAD, F. (2011). The Riparian Alder Forests of the Sopron Hills. *Acta Silvatica & Lignaria Hungarica* 7: 109–124.
- SZÜCS, P. & SZMORAD, F. (2009). Ergänzungen zur Moosflora des Ödenburger Gebirges. *Flora Pannonica* 7: 61–72.
- ZECHMEISTER, H.G. (2004). Die Moosflora im Natura 2000 Gebiet "Neusiedlersee", unter besonderer Berücksichtigung der Salzwiesen im Seewinkel. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 141: 43–62.
- ZECHMEISTER, H.G. (2005a). Bryophytes of continental salt meadows in Austria. *Journal of Bryology* 27: 297–302.
- ZECHMEISTER, H.G. (2005b). Die Moosflora der Serpentinrasen im Burgenland. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 142: 9–15.
- ZECHMEISTER, H.G. (2008). Vorkommen und Gefährdung der Torfmoose (Gattung *Sphagnum* L.) im Burgenland. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 145: 97–106.
- ZECHMEISTER, H.G., HAGEL, H., GENDO, A., OSVALDIK, V., PATEK, M., PRINZ, M., SCHRÖCK, C. & KÖCKINGER, H. (2013). Die Rote Liste der Moose Niederösterreichs. *Wissenschaftliche Mitteilungen Niederösterreichisches Landesmuseum* 24: 4–126.

(submitted: 30.11.2015, accepted: 04.01.2016)

APPENDIX

Site details

1. Burgenland, Bezirk Oberpullendorf, Ritzing, Angerwald, near country border, planted *Picea abies* forest (21.10.2009) N47°38'24.7" E16°29'43.9", 477 m. [8364.4]
2. Burgenland, Bezirk Oberpullendorf, Ritzing, Angerwald, near country border, *Fagus sylvatica* forest (22.10.2009) N47°38'21.9" E16°30'4.0", 472 m. [8365.3]
3. Burgenland, Bezirk Oberpullendorf, Ritzing, near village, on gravelly forest road (23.07.2013) N47°38'33.9" E 16°28'19.4", 430 m. [8364.4]
4. Burgenland, Bezirk Oberpullendorf, Ritzing, near village, next to gravelly forest road (23.07.2013) N47°38'34.9" E16°28'17.0", 433 m. [8364.4]
5. Burgenland, Bezirk Oberpullendorf, Ritzing, lake (23.07.2013) N47°38'45.5" E16°28'11.0", 436 m. [8364.4]
6. Burgenland, Bezirk Oberpullendorf, Ritzing, on embankment of forest road (23.07.2013) N47°38'57.7" E16°28'16.7", 478 m. [8364.4]
7. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (23.07.2013) N47°38'57.7" E16°28'16.7", 481 m. [8364.4]
8. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, by forest road (23.07.2013) N47°38'58.1" E16°27'59.0", 525 m. [8364.4]
9. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest (23.07.2013) N47°39'01.1" E16°27'50.2", 552 m. [8364.2]
10. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, by forest road (23.07.2013) N47°39'01.6" E16°27'37.8", 544 m. [8364.2]
11. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (23.07.2013) N47°39'04.2" E16°27'37.0", 543 m. [8364.2]
12. Burgenland, Bezirk Oberpullendorf, Ritzing, on embankment of forest road (23.07.2013) N47°39'01.2" E16°27'32.9", 526 m. [8364.2]
13. Burgenland, Bezirk Oberpullendorf, Ritzing, in old *Fagus sylvatica* forest (23.07.2013) N47°38'57.7" E16°27'33.2", 518 m. [8364.4]
14. Burgenland, Bezirk Oberpullendorf, Ritzing, near lake, by stream (23.07.2013) N47°38'55.20.0" E16°27'28.0", 494 m. [8364.4]
15. Burgenland, Bezirk Oberpullendorf, Ritzing, by stream (23.07.2013) N47°38'52.6" E16°27'30.9", 482 m. [8364.4]
16. Burgenland, Bezirk Oberpullendorf, Ritzing, dried puddles (23.07.2013) N47°38'41.0", E16°27'36.3", 467 m. [8364.4]
17. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (23.07.2013) N47°38'38.5", E16°27'41.7", 459 m. [8364.4]
18. Burgenland, Bezirk Oberpullendorf, Ritzing, grassland (23.07.2013) N47°38'30.8", E16°27'58.2", 415 m. [8364.4]
19. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, by the forest road (23.07.2013) N47°38'24.2", E16°28'6.4", 422 m. [8364.4]
20. Burgenland, Bezirk Oberpullendorf, Ritzing, grassland (23.07.2013) N47°38'17.3" E16°28'10.6", 393 m. [8364.4]
21. Burgenland, Bezirk Oberpullendorf, Ritzing, Waldschule, by the road (23.07.2013) N47°38'33.0" E16°28'32.4", 416 m. [8364.4]
22. Burgenland, Bezirk Oberpullendorf, Ritzing, old *Fagus sylvatica* forest, by the forest road (26.10.2013) N47°38'45.8" E16°28'57.4", 482 m. [8364.4]
23. Burgenland, Bezirk Oberpullendorf, Ritzing, old *Fagus sylvatica* forest (26.10.2013) N47°38'42.7" E16°28'58.6", 491 m. [8364.4]
24. Burgenland, Bezirk Oberpullendorf, Ritzing, Lange Zeile, embankment of forest road (26.10.2013) N47°38'33.1" E16°28'59.0", 486 m. [8364.4]
25. Burgenland, Bezirk Oberpullendorf, Ritzing, Lange Zeile, crossroads (26.10.2013) N47°38'28.0" E16°29'1.40", 486 m.

26. Burgenland, Bezirk Oberpullendorf, Ritzing, border of coniferous forest (26.10.2013) N47°38'25.6" E16°28'50.0", 481 m. [8364.4]
27. Burgenland, Bezirk Oberpullendorf, Ritzing, in coniferous forest (26.10.2013) N47°38'27.1" E16°28'41.1", 449 m. [8364.4]
28. Burgenland, Bezirk Oberpullendorf, Ritzing, in little valley (26.10.2013) N47°38'31.2" E16°28'44.9", 434 m. [8364.4]
29. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of road, in wheel-tack (26.10.2013) N47°38'39.6" E16°28'45.2", 432 m. [8364.4]
30. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of road, in wheel-tack (26.10.2013) N47°38'40.4" E16°28'46.5", 435 m. [8364.4]
31. Burgenland, Bezirk Oberpullendorf, Ritzing, in old *Fagus sylvatica* forest (28.10.2013) N47°38'39.2" E16°29'5.1", 502 m. [8364.4]
32. Burgenland, Bezirk Oberpullendorf, Ritzing, in old *Fagus sylvatica* forest (28.10.2013) N47°38'30.7" E16°29'12.0", 512 m. [8364.4]
33. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, embankment of forest road (28.10.2013) N47°38'9.1" E16°29'6.8", 486 m. [8364.4]
34. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, embankment of forest road (28.10.2013) N47°38'9.1" E16°29'6.8", 472m. [8364.4]
35. Burgenland, Bezirk Oberpullendorf, Ritzing, border of grassland (28.10.2013) N47°37'35.7" E16°29'25.5", 379 m. [8364.4]
36. Burgenland, Bezirk Oberpullendorf, Ritzing, grassland (28.10.2013) N47°37'33.2" E16°29'31.0", 370 m. [8364.4]
37. Burgenland, Bezirk Oberpullendorf, Ritzing, grassland, stream (28.10.2013) N47°37'50.4" E16°29'27.7", 399 m. [8364.4]
38. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, embankment of forest road (28.10.2013) N47°38'2.8" E16°29'9.8", 471 m. [8364.4]
39. Burgenland, Bezirk Oberpullendorf, Ritzing, *Pinus sylvestris* forest, in glade (28.10.2013) N47°37'54.0" E16°29'30.6", 421 m. [8364.4]
40. Burgenland, Bezirk Oberpullendorf, Ritzing, *Pinus sylvestris* forest, in glade (28.10.2013) N47°37'54.1" E16°29'34.6", 444 m. [8364.4]
41. Burgenland, Bezirk Oberpullendorf, Ritzing, *Pinus sylvestris* forest, in glade (28.10.2013) 47°37'54.1" 16°29'34.5", 444 m. [8364.4]
42. Burgenland, Bezirk Oberpullendorf, Ritzing, *Pinus sylvestris* forest, in glade (28.10.2013) N47°37'54.2" E16°29'38.2", 456 m. [8364.4]
43. Burgenland, Bezirk Oberpullendorf, Ritzing, border of *Pinus sylvestris* forest, by forest road (28.10.2013) N47°37'53.0" E16°29'42.9", 450 m. [8364.4]
44. Burgenland, Bezirk Oberpullendorf, Ritzing, arable field (28.10.2013) N47°37'33.9" E16°29'58.2", 398 m. [8364.4]
45. Burgenland, Bezirk Oberpullendorf, Ritzing, arable field (28.10.2013) N47°37'29.9" E16°30'9.4", 395 m. [8365.3]
46. Burgenland, Bezirk Oberpullendorf, Ritzing, valley, by stream (28.10.2013) N47°37'39.1" E16°30'26.2", 367 m. [8365.3]
47. Burgenland, Bezirk Oberpullendorf, Ritzing, valley, by stream (28.10.2013) N47°37'40.4" E16°30'24.1", 368 m. [8365.3]
48. Burgenland, Bezirk Oberpullendorf, Ritzing, gravelly road crossing (28.10.2013) N47°37'43.5" E16°30'22.4", 360 m. [8365.3]
49. Burgenland, Bezirk Oberpullendorf, Ritzing, valley, by stream (28.10.2013) N47°37'44.9" E16°30'17.4", 371 m. [8365.3]
50. Burgenland, Bezirk Oberpullendorf, Ritzing, valley, by stream (28.10.2013) N47°37'45.5" E16°30'12.1", 371 m. [8365.3]
51. Burgenland, Bezirk Oberpullendorf, Ritzing, valley, by stream (28.10.2013) N47°37'47.4" E16°30'10.4", 378 m. [8365.3]
52. Burgenland, Bezirk Oberpullendorf, Ritzing, valley, by stream (28.10.2013) N47°37'48.5" E16°30'08.6", 383 m. [8365.3]

53. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of forest road (28.10.2013) N47°37'53.3" E16°30'08.6", 401 m. [8365.3]
54. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road, little lake (28.10.2013) N47°38'05.8" E16°29'46.5", 449 m. [8364.4]
55. Burgenland, Bezirk Oberpullendorf, Ritzing, wet grassland (28.10.2013) N47°37'59.0" E16°29'20.4", 418 m. [8364.4]
56. Burgenland, Bezirk Oberpullendorf, Ritzing, wet grassland (28.10.2013) N47°38'00.4" E16°29'20.0", 421 m. [8364.4]
57. Burgenland, Bezirk Oberpullendorf, Ritzing, calcareous spring (28.10.2013) N47°38'05.6" E16°29'18.6", 447 m. [8364.4]
58. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (28.10.2013) N47°38'07.3" E16°29'19.9", 510 m. [8364.4]
59. Burgenland, Bezirk Oberpullendorf, Ritzing, Angerwald, near country border, deciduous forest (30.10.2013) N47°38'29.3" E16°29'27.1", 521 m. [8364.4]
60. Burgenland, Bezirk Oberpullendorf, Ritzing, Angerwald, near country border, deciduous forest (30.10.2013) N47°38'31.8" E16°29'34.5", 519 m. [8364.4]
61. Burgenland, Bezirk Oberpullendorf, Ritzing, near country border, embankment of forest road (30.10.2013) N47°38'21.3" E16°30'15.9", 451 m. [8365.3]
62. Burgenland, Bezirk Oberpullendorf, Ritzing, Gruberkreuz, near country border, forest road crossing, little lake (30.10.2013) N47°38'16.9" E16°30'24.0", 445 m. [8365.3]
63. Burgenland, Bezirk Oberpullendorf, Ritzing, abandoned gneis-stone quarry (30.10.2013) N47°38'35.5" E16°31'08.8", 440 m. [8365.3]
64. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of forest road (30.10.2013) N47°38'20.1" E16°31'23.8", 445 m. [8365.3]
65. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (30.10.2013) N47°37'59.4" E16°31'40.0", 345 m. [8365.3]
66. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of forest road (30.10.2013) N47°37'58.2" E16°31'42.5", 365 m. [8365.3]
67. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of forest road (30.10.2013) 47°37'34.6" E16°31'58.2", 330 m. [8365.3]
68. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (30.10.2013) N47°37'41.7" E16°31'45.3", 340 m. [8365.3]
69. Burgenland, Bezirk Oberpullendorf, Ritzing, abandoned quarry, recultivated places (30.10.2013) N47°37'41.7" E16°31'45.3", 340 m. [8365.3]
70. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of forest road (30.10.2013) N47°37'30.1" E16°32'03.1", 325 m. [8365.3]
71. Burgenland, Bezirk Oberpullendorf, Neckenmarkt, fence of garden (30.10.2013) N47°37'10.6" E16°32'27.1", 290 m. [8365.3]
72. Burgenland, Bezirk Oberpullendorf, Neckenmarkt, weekend houses (30.10.2013) N47°37'13.1" E16°32'21.9", 300 m. [8365.3]
73. Burgenland, Bezirk Mattersburg, Marz, near recultivated quarry, by forest road (22.11.2013) N47°42'16.8" E16°23'47.1", 465 m. [8264.3]
74. Burgenland, Bezirk Mattersburg, Siegraben, by stream (22.11.2013) N47°40'22.7" E16°23'54.6", 380 m. [8364.1]
75. Burgenland, Bezirk Mattersburg, Siegraben, wet grassland (22.11.2013) N47°40'22.9" E16°23'55.8", 375 m. [8364.1]
76. Burgenland, Bezirk Mattersburg, Siegraben, wet grassland (22.11.2013) N47°40'22.4" E16°23'58.1", 385 m. [8364.1]
77. Burgenland, Bezirk Mattersburg, Siegraben, wetland and stream (22.11.2013) N47°40'21.9" E16°24'02.3", 380 m. [8364.1]
78. Burgenland, Bezirk Mattersburg, Siegraben, wetland and stream (22.11.2013) N47°40'20.7" E16°24'06.1", 385 m. [8364.1]
79. Burgenland, Bezirk Mattersburg, Siegraben, embankment of forest (22.11.2013) N47°40'18.6" E16°24'03.6", 400 m. [8364.1]

80. Burgenland, Bezirk Mattersburg, Sieggraben, by forest road, little pond (22.11.2013) N47°40'18.8" E16°23'59.5", 395 m. [8364.1]
81. Burgenland, Bezirk Mattersburg, Sieggraben, near forest road (22.11.2013) N47°40'18.6" E16°24'03.6", 395 m. [8364.1]
82. Burgenland, Bezirk Mattersburg, Sieggraben, valley, by stream (22.11.2013) N47°39'36.5" E16°22'53.1", 500 m. [8364.1]
83. Burgenland, Bezirk Mattersburg, Sieggraben, Satterhöhe, valley, by stream (22.11.2013) N47°39'43.5" E16°22'49.3", 470 m. [8364.1]
84. Burgenland, Bezirk Mattersburg, Sieggraben, border of grassland, embankment of forest road (22.11.2013) N47°39'46.7" E16°22'53.2", 455 m. [8364.1]
85. Burgenland, Bezirk Mattersburg, Sieggraben, valley, by stream (22.11.2013) N47°39'40.6" E16°22'52.9", 475 m. [8364.1]
86. Burgenland, Bezirk Mattersburg, Sieggraben, roadside (22.11.2013) N47°39'34.0" E16°22'45.1", 495 m. [8364.1]
87. Burgenland, Bezirk Mattersburg, Kalkgraben, grassland and roadside (22.11.2013) N47°39'40.6" E16°22'52.9", 455 m. [8364.1]
88. Burgenland, Bezirk Mattersburg, Kalkgraben, grassland (22.11.2013) N47°39'40.6" E16°22'52.9", 420 m. [8364.1]
89. Burgenland, Bezirk Oberpullendorf, Neckenmarkt, Millenium Teich, between two lakes (24.06.2014) N47°36'59.1" E16°34'05.0", 235 m. [8365.3]
90. Burgenland, Bezirk Oberpullendorf, Neckenmarkt, embankment of forest road (24.06.2014) N47°37'33.2" E16°33'30.7", 335 m. [8365.3]
91. Burgenland, Bezirk Oberpullendorf, Neckenmarkt, near embankment of forest road, deciduous forest (24.06.2014) N47°37'33.8" E16°33'27.4", 350 m. [8365.3]
92. Burgenland, Bezirk Oberpullendorf, Ritzing, in glade, grass, on soil (30.07.2014) N47°39'07.6" E16°27'20.4", 545 m. [8364.2]
93. Burgenland, Bezirk Oberpullendorf, Ritzing, in mixed forest (30.07.2014) N47°38'54.2" E16°27'03.6", 565 m. [8364.4]
94. Burgenland, Bezirk Oberpullendorf, Ritzing, in mixed forest (30.07.2014) N47°38'46.5" E16°26'56.4", 545 m. [8364.4]
95. Burgenland, Bezirk Oberpullendorf, Ritzing, in glade of planted pine forest, grass (30.07.2014) N47°38'20.1" E16°26'43.2", 440 m. [8364.4]
96. Burgenland, Bezirk Oberpullendorf, Ritzing, next of planted pine forest, by forest road (30.07.2014) N47°38'15.5" E16°26'46.8", 420 m. [8364.4]
97. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (30.07.2014) N47°38'10.2" E16°26'41.7", 405 m. [8364.4]
98. Burgenland, Bezirk Oberpullendorf, Ritzing, wall of road cut (30.07.2014) N47°38'07.9" E16°26'43.7", 420 m. [8364.4]
99. Burgenland, Bezirk Oberpullendorf, Ritzing, in coniferous forest (30.07.2014) N47°38'07.2" E16°26'45.0", 445 m. [8364.4]
100. Burgenland, Bezirk Oberpullendorf, Ritzing, in coniferous forest (30.07.2014) N47°38'07.9" E16°26'42.8", 445 m. [8364.4]
101. Burgenland, Bezirk Oberpullendorf, Ritzing, on embankment of forest road (30.07.2014) N47°38'06.8" E16°26'36.9", 410 m. [8364.4]
102. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (30.07.2014) N47°38'06.1" E16°26'35.4", 410 m. [8364.4]
103. Burgenland, Bezirk Oberpullendorf, Ritzing, on embankment of road (30.07.2014) N47°38'05.2" E16°26'35.3", 410 m. [8364.4]
104. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (30.07.2014) N47°38'08.8" E16°26'33.6", 395 m. [8364.4]
105. Burgenland, Bezirk Oberpullendorf, Ritzing, embankment of forest road (30.07.2014) N47°38'10.1" E16°26'33.2", 405 m. [8364.4]
106. Burgenland, Bezirk Oberpullendorf, Ritzing, in *Alnus glutinosa* marsh (30.07.2014) N47°38'09.9" E16°26'31.8", 400 m. [8364.4]

107. Burgenland, Bezirk Oberpullendorf, Ritzing, by stream, water conversancy building (30.07.2014) N47°38'09.3" E16°26'29.8", 400 m. [8364.4]
108. Burgenland, Bezirk Oberpullendorf, Ritzing, by stream (30.07.2014) N47°38'10.3" E16°26'29.3", 400 m. [8364.4]
109. Burgenland, Bezirk Oberpullendorf, Ritzing, in *Alnus glutinosa* marsh (30.07.2014) N47°38'10.8" E16°26'30.9", 405 m. [8364.4]
110. Burgenland, Bezirk Oberpullendorf, Ritzing, by stream (30.07.2014) N47°38'11.6" E16°26'26.8", 400 m. [8364.4]
111. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (31.07.2014) N47°39'14.7" E16°26'38.9", 495 m. [8364.2]
112. Burgenland, Bezirk Oberpullendorf, Ritzing, by forest road (31.07.2014) N47°39'04.7" E16°26'38.1", 480 m. [8364.2]
113. Burgenland, Bezirk Oberpullendorf, Ritzing, by wet places (31.07.2014) N47°39'1.6" E16°26'26.6", 465 m. [8364.2]
114. Burgenland, Bezirk Oberpullendorf, Ritzing, near planted *Picea abies* forest, by forest road (31.07.2014) N47°38'49.9" E16°26'04.1", 460 m. [8364.4]
115. Burgenland, Bezirk Oberpullendorf, Ritzing, by stream, on milestone (31.07.2014) N47°38'12.5" E16°26'25.6", 405 m. [8364.4]
116. Burgenland, Bezirk Oberpullendorf, Ritzing, by road-crossing, monument (31.07.2014) N47°37'57.6" E16°26'21.3", 385 m. [8364.4]
117. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, couloir (31.07.2014) N47°38'41.2" E16°27'7.3", 525 m. [8364.4]
118. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, (31.07.2014) N47°38'40.1" E16°27'4.8", 515 m. [8364.4]
119. Burgenland, Bezirk Oberpullendorf, Ritzing, in deciduous forest, by forest road (31.07.2014) N47°38'39.9" E16°26'49.6", 530 m. [8364.4]
120. Burgenland, Bezirk Oberpullendorf, Ritzing, in road-crossing (31.07.2014) N47°39'03.4" E16°27'5.9", 540 m. [8364.2]