Johannes Hedwig and the founding of modern bryology

Michelle J. Price1, 2

1Conservatory and Botanical Garden of the City of Geneva, Chemin de l'Impératrice 1, 1292 Chambésy, Geneva, Switzerland. 2Department of Botany and Plant Sciences, University of Geneva, Quai Ernest-Ansermet 30, 1211 Geneva, Switzerland (michelle.price@ville-ge.ch)

Johannes Hedwig (1730-1799), one of the founding fathers of modern bryology, was a pioneer of his time. He maintained an impeccably organized herbarium, described 82 mosses that were new to science and greatly increased the number of moss genera in use at the time, effectively beginning the process of scientific recognition of moss diversity. Above and beyond these taxonomic contributions, however, he revolutionized the bryological thinking of his era, detailing different morphological structures in mosses, as observed under the microscope. He later used features to group and classify them (presence/absence of an operculum or a peristome, peristomes with one or two rows of teeth), introducing a substantial number of concepts or terms into the bryological lexicon along the way that we still use today (antheridia, sporangium, spore). A practicing medical doctor for many years in Chemnitz, Hedwig studied and collected plants, including bryophytes, in his free time. After receiving a microscope from J.D. Schreber sometime around 1760 he became interested in the features and functioning of structures in smaller and smaller organisms. Realizing that microscope-based observations revealed natural variations and traits of scientific importance, around 1770 he learnt to draw and began to illustrate his findings. His original illustrations accompany his works and they are a great testament to both his observational and illustration skills. He was interested in the natural history of mosses (Fundamentum historiae naturalis muscorum frondosorum) and also studied the reproduction and reproductive organs of cryptogams more generally (Theoria generationis et fructificationis plantarum cryptogamicarum). He went on to produce a four volume series containing detailed descriptions and illustrations of the mosses known to him (Descripition et adumbration microscope-analytica muscorum frondosorum) before embarking on what would become his posthumous magnum opus Species muscorum frondosorum, a work that was finished by his student C.F. Schwägrichen for publication in 1801. Hedwig’s body of work has had a long lasting influence on our particular branch of science, not only as his 1801 work is the designated starting point of the nomenclature of mosses (expecting the Sphagnaceae), but also due to the perspicacity of his observations of morphological features in the mosses.

Keywords: bryology, morphology, microscopes, classification, Johannes Hedwig.
Oral Presentation

**Kurt Goebel, George and Andreas Schimper: their eclectic contributions to bryophyte biology**

Jeffrey G Duckett

Life Sciences, Plants Division, Natural history Museum, Cromwell Road, London, SW7 5BD, UK

j.g.duckett@qmul.ac.uk

Most of the founding fathers of bryology are remembered for what might best be described as floristic works viz. species descriptions and illustrations and floras that we all rely on and indeed take for granted today. Kurt Goebel (1855-1932), George Schimper (1804-1878) and his son Andreas' (1856-1901), most important contributions to bryophyte biology are somewhat different and have important implications today far beyond that envisioned when the original studies were carried out. Perusal of the beautiful illustrations in the 6 volumes of B.S. & G., for which George Schimper is best known as the ‘S’, reveal the only illustrations of the paraphyses in a multitude of taxa and dextral coiling of peristomes across mosses whereas the setae switch from sinistral at the base to dextral immediately below the capsules. His uncannily accurate description of stem ontogeny in *Sphagnum* is a supreme model for plant anatomists whose reinvestigation in recent years led to the discovery that *Sphagnum* stems contain food-conducting cells with organelles aligned along longitudinal arrays of endoplasmic microtubules like those in peristomate mosses. His son Andreas gave the first descriptions of plastids, and then went on to explain the interconversion of the different types and showed their transmission through germ cells (the eggs of hornworts). In 1883 he postulated the endosymbiotic origin of chloroplasts, long before this notion gained general credence in the 1960s. Goebel was a student of Hofmeister who must certainly have influenced his lifelong interests in morphology comparative functional anatomy, and the developmental physiology of plants particularly in phylogenetic contexts. Perhaps one of the greatest services to non-German speaking botanists was the translation of his book ‘Organography of Plants’ by Balfour in 1905. In this book we find a compilation of just about everything known at that time about how plants work with significant amounts of coming from his own research which included a meticulous description of the fungal endophyte in *Trebia*. Ultrastructural re-examination this association followed by experimental and molecular studies have now led to the establishment of mucoromycote fungi as probably the earliest symbionts at the dawn of land plant evolution.
Spruce was interested in botany since his childhood. He was a paragon of Victorian age scientists, having multiple talents, becoming familiar not only with vascular and cryptogamic botany, but also with tropical crops (like quinine and the rubber plant), ethnography, linguistics, geography and geology, and being an amateur musician. He was contemporary of Humboldt, Martius, Darwin and Wallace. His first major bryological work was *The Musci and Hepaticae of the Pyrenees* (1850), including a new genus (*Southbya*). Encouraged by Hooker and Bentham, he went to Brazil, Peru and Ecuador, to collect plants for Kew Garden. His expedition, through the tributaries of Amazon River and the Andes to the Pacific coasts, lasted for 15 years (1849-1864) and resulted in an enormous number of bryophytes, more than 7000 vascular plant species, seedlings and seeds of rubber and quinin trees and a lot of economic, ethnographic, geologic and linguistic observations, but cost him his health and fortune. His magnum opus, after publishing the *Palmae Amazonicae* (1869), was *Hepaticae Amazonicae et Andinae* (1884-85), in which he described near 400 species and 4 genera new to science. The greatest taxonomic significance of this work was the subdivision of genus *Frullania* in up to 6 still valid subgenera and the division of the giga-genus *Lejeunea* into 39 subgenera. The majority of these gained generic rank and form today the basis of the classification of the Lejeuneaceae. His strenuous efforts to make valuable plant collections under difficult conditions and many adventures were documented in his diary and letters, edited after his death by his friend, Alfred Russell Wallace. His liverwort specimens, processed by himself, are deposited in Manchester herbarium (MA), his moss collection, identified by Mitten, in the New York Botanical Garden herbarium (NY), while his vascular plant collections are in Kew Garden herbarium (K) with duplicates in numerous other herbaria.

**Keywords:** Brazil, Ecuador, Peru, liverworts, taxonomy
Victor Ferdinand Brotherus' contribution to world diversity of mosses

Timo Koponen
University of Helsinki, Finland (timo.koponen@helsinki.fi)

Finnish bryologist V. F. Brotherus (1849–1929) became internationally known after his thesis for Ph.D. “Études sur la distribution des mousses au Caucase.” (1884) and his “Enumeratio muscorum Caucasi” (1892) were published. He began to get letters from botanists and expeditions asking him to identify their collections. Brotherus became soon known of his ability to identify the specimens from exotic areas such as Japan, the Philippines, Australia, and Argentine and publish the material quickly. His fame was later confirmed when Adolf Engler (1844–1930) asked him to write the major part of “Musci” for “Die naturlichen Pflanzenfamilien” (1901–1909). The classification system in the 1st edition was old fashioned, and A. Engler requested Brotherus to adopt M. Fleischer’s (1900–1922) phylogenetic system for the 2nd edition (1924, 1925). At the same time with the 2nd edition, he wrote the flora “Die Laubmoose Fennoscandias” (1923) and studied the material from China collected by H. Handel-Mazzetti (1882–1940). These were published in “Musci” in Handel-Mazzetti’s series “Symbolae sinicae” (1929). Altogether Brotherus published 176 articles or books, and described c. 80 genera and c. 1800 species of mosses. His collection of letters, preserved in the library of the University of Helsinki, contains 4751 letters from 504 different persons.
The dawn of bryology in North America: a tale of a cursed flora

Bernard Goffinet¹, Rafael Medina²

¹ Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, U.S.A. (bernard.goffinet@uconn.edu); ² Department of Biology, Augustana College, Rock Island, IL 61201 U.S.A.

The Manual of the Mosses of North America, written by Léo Lesquereux and Thomas Potts James in 1884, was the first attempt to complete a comprehensive moss flora of the United States and a key milestone in the botany of the country. The history of this work, however, involves a long process that spans almost four decades and that was compromised by the different life circumstances of everyone involved. Perhaps the most eloquent anecdote that illustrates the long development of this book is the one recovered by Elizabeth Britton in a note written in 1924 and found in a specimen of NY: she was told that the Manual was published “by a man who knew nothing of mosses, for a blind man, and a dead man”. Using this quote as a prompt we explore biographic and epistolary sources to understand the history of the development of this flora starting when it was first commissioned to William Sullivant by Asa Gray. The members of the “Sullivant circle”, and in particular the partnership between the latter and Lesquereux, are behind the first golden period of the study of bryophytes in the United States.

Keywords: United States, Sullivant, Lesquereux, James, Britton
International collaboration among bryologists, commonplace today, has a long history that spans almost two hundred years. The article on the moss genus Spiridens by Christian G. D. Nees von Esenbeck from Bonn and Carl G.C. Reinwardt from Leiden may be considered the first international bryological publication. The first major international undertakings, with participation of bryologists from different nations, were Bryologia Europaea (1836-1851) spearheaded by Wilhelm Philipp Schimper in Strasbourg and Synopsis Hepaticarum (1844-147) initiated by Christian G. D. Nees von Esenbeck. These works are the culminations of the "Golden Period" of bryophyte morphology and taxonomy around the mid-19th century. In the first half of the 20th century international collaboration was promoted by Frans Verdoorn in Utrecht through Annales Bryologici (1927-1939), the first bryological journal with an international editorial board, and the multi-authored Manual of Bryology (1932) with contributions from six nations. In 1966, at the Pacific Science Congress in Hawaii, William C. Steere (U.S.A.) together with Stanley W. Greene (U.K.) and Zennoske Iwatsuki (Japan) took the initiative towards the establishment of an International Association of Bryologists, founded three years later in Seattle. Several multinational endeavors were successfully promoted by the organization, which this year celebrates its golden jubilee. Today, technological advances have enabled a multitude of international projects, resulting in major advances in the field. Nevertheless, fruitful international collaboration remains a challenge that requires active communication, creativity, friendship, flexibility and enthusiasm.

Keywords: communication, creativity, enthusiasm, flexibility, friendship
Genetic and morphological differentiation in the genus *Conocephalum* (Hepatics).

Hiroyuki Akiyama\textsuperscript{1}, Ireneusz J. Odrzykoski\textsuperscript{2}

\textsuperscript{1}Museum of Nature and Human Activities, Hyogo/ Institute of Nature and Environmental Sciences, University of Hyogo, Yayoigaoka-6, Sanda, Hyogo 669-1546, JAPAN; \textsuperscript{2}Department of Genetics, Institute for Experimental Biology, Adam Mickiewicz University, 61-614 Poznań, Umultowska 89, Poland.

The genus *Conocephalum* Hill is a sole member of the Conocephalaceae (Marchantiidae). It includes three species, i.e., pan boreal *C. salebrosum*, European *C. conicum* (L.) Dumort. and East Asia endemic *C. japonicum* (Thunb.) Grolle. A number of studies using allozymes and DNA sequences (*rbcl, psbA*), revealed unexpected complex structure and nowadays it is widely accepted that there are probably three additional species in *C. conicum* complex (A, F, J) and three in *C. japonicum* (JN, JS and CS). Though they are highly differentiated and thus should be treated as different species, only the *C. conicum* "S" has been described as separate species, *C. salebrosum*. Inter-relationship among these cryptic species especially for A, F, and J, is ambiguous because of limited sampling. We used *rbcl+rps4* sequences to study distinctiveness of each cryptic species and their exact inter-relationship. Samples used in this study were from the long-cultivated strains maintained in Poland as well as newly gathered ones mainly from Japan and Taiwan. As a result, presence of total six species in *C. conicum* and three in *C. japonicum* were confirmed. Among them, there is one additional species previously recognized as *C. conicum* R (Miwa et al. 2009) or *C. conicum* Type III (Toyota 1994, Kim et al. 2001); it is analyzed as being sister to the rest of five species. It has unique metabolic and morphological features, such as presence of trans-methyl cinnamate in natural conditions and absence of mucilage cavity in the central part of thallus. Based on DNA haplotypes, we examined morphological features and distributional patterns of the three cryptic species (C. conicum F, J, R) and *C. salebrosum* distributed in the Japanese Archipelago. Each species shows separate distributional pattern well coincided to climate and soil pattern.

Keywords: *Conocephalum conicum*, *C. salebrosum*, *C. japonicum*, genetic differentiation
UV tolerance in Mojave Desert biocrust mosses

Jenna T. B. Ekwealor¹, Suzanne Kosina², Trent Northen², Brent D. Mishler¹

¹ Department of Integrative Biology and University and Jepson Herbaria, University of California, Berkeley, Berkeley, CA 94720, U.S.A. (jtbe@berkeley.edu); ² Lawrence Berkeley National Laboratory, Berkeley, CA 94720, United States

Terrestrial mosses dehydrate and go dormant between precipitation events. Although many mosses are found in cool, low light environments, a number are abundant in drylands. We investigated the effects of ultraviolet (UV) radiation on desert mosses Syntrichia caninervis and S. ruralis. These species are highly desiccation tolerant; they can lose almost all of their cellular water and recover after rehydration. In nature, desert mosses not only have to withstand the damage of desiccation itself but must also be able to recover from any damage incurred while inert, or have adequate mechanisms for injury prevention. They have no ability for active repair when dry and face risk of damage to sensitive molecules, including DNA, which absorbs UV wavelengths. We used transcriptomics, metabolomics, chlorophyll fluorescence, and morphological measurements in field and laboratory experiments to better understand the dimensions of UV tolerance in Syntrichia. Transcriptomes were compared for differential expression and to identify candidate genes. A growth chamber experiment was performed to test the metabolomic effects of UV radiation and desiccation. Liquid chromatography mass spectroscopy was used to characterize metabolites that are differentially produced and that absorb UV. Finally, 40 naturally occurring patches of S. caninervis were covered with UV-filtering (>80% reduction) or UV-transmitting (>80% transmission) windows. After one year, patches were compared for key metabolites and transcripts, while chlorophyll fluorescence was used to measure stress. These field and laboratory experiments uncover detailed information about these plants’ response to UV and desiccation, improving our understanding of how they tolerate high levels of UV radiation while desiccated.

Keywords: UV tolerance, desiccation tolerance, adaptation, photobiology
From the South to the North – The evolutionary history of the simple thalloid liverwort Metzgeria (Metzgeriaceae, Jungermanniopsida)

Julia Bechteler¹, Martin Nebel¹, Karola Maul¹, Alfons Schäfer-Verwimp³, Nicole Schütz², Dietmar Quandt¹

¹ Nees Institute for Biodiversity of Plants, University of Bonn, Meckenheimer Allee 170, Bonn 53115, Germany (bechteler@uni-bonn.de); ² Department of Botany, Natural History Museum Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany; ³ Mittlere Letten 11, 88634 Herdwangen-Schönach, Germany

Most studies that deal with the evolution of epiphytic liverworts focused on leafy liverworts. Here we employ the study system Metzgeria to investigate the historical biogeography of the only epiphytic thalloid liverwort genus. Metzgeria has a worldwide distribution with hotspots of diversity in the southern hemisphere, particularly the Neotropics and Australasia. Currently there are around 100 species accepted of which we could include about 40%, covering its full geographic range. We used Maximum likelihood and Bayesian analyses on a chloroplast dataset (trnL-trnF, rps4, rpl16) to infer the phylogeny of Metzgeria. Divergence times were estimated with a Bayesian relaxed clock approach and the fossil Metzgeriothallus sharonae (Late Middle Devonian, 387-382 Ma). Ancestral areas were estimated in BioGeoBEARS. Metzgeria likely originated in the Permian and its crown group diversification took place in the Cretaceous, followed by Cenozoic radiations. The evolutionary history of Metzgeria was shaped by ancient Gondwana vicariance and subsequent dispersal events to the Northern hemisphere.

Keywords: Epiphytic liverworts, Gondwana vicariance, dispersal, southern hemisphere distribution, historical biogeography
Presentation type: Oral Presentation, Poster Presentation

Functional traits related to growth and decomposition in *Sphagnum*

Fia Bengtsson

1 Department of Plant Ecology and Evolution, Uppsala University, Norbyvägen 18D, SE-75236 Uppsala, Sweden. fia.aurelia@gmail.com

Net primary productivity of northern peatlands is relatively low, but in combination with slow decomposition it has led to extensive postglacial storage of carbon in peat. Peatmosses (*Sphagnum*) are ecosystem engineers that largely govern carbon sequestration in these ecosystems. My thesis concerned functional traits in *Sphagnum* species, and I will present the parts of this work addressing three questions: (I) Are growth, photosynthesis and decomposition, and the trade-offs between these traits related to habitat or phylogeny? (II) What are the determinants of decomposition and are there trade-offs between metabolites that affect decomposition? (III) How do macro-climate and local environment determine growth in *Sphagnum* across the Holarctic?

We found support for a trade-off between growth and decay resistance, but innate qualities translated differently to field responses in different species. There were no trade-offs between production of different decay-affecting metabolites (soluble phenolics, lignin-like phenolics and the cell-wall carbohydrate sphagnan), instead, the species with lower decomposition had more of all these. We found that metabolite production was constrained by phylogeny, but the effects of the metabolites on decay were modified by nutrient availability in the habitat. Precipitation, temperature and vascular plant cover were the best predictors of the growth of two species (with different functional traits) across the Holarctic. In a changing climate, *S. fuscum* will retain its carbon uptake, while *S. magellanicum* will decrease its carbon uptake if a warmer climate coincides with less precipitation.

My work has advanced the emerging field of trait ecology in *Sphagnum* revealing an ever more complex picture of *Sphagnum* ecology. Also, the data offer opportunities for improvements of peatland ecosystem models. Functional trait-relationships are necessary for understanding the long-term dynamics of peatland communities; in a changing world such relationships will affect carbon sequestration and management of carbon stocks.

Keywords: northern peatlands, *Sphagnum*, functional traits, productivity, litter decomposition
The rare male enigma in bryophytes – what do geographic scales, environment and life histories tell

Irene Bisang¹, Johan Ehrlén², Lars Hedenäs¹

¹ Department of Botany, Swedish Museum of Natural History, Box 1005, SE-104 05 Stockholm, Sweden (irene.bisang@nrm.se); ²Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden.

The female bias in adult sex ratios in unisexual bryophytes that are reproductive remains intriguing. In most cases, it is unresolved whether it is due to more female than male genotypes (genotypic) or higher proportions of sex expressing females (phenotypic). Previous sex ratio studies have mainly dealt with species in dry habitats, or with species of disturbed habitats that grow fast and freely reproduce sexually in cultivation. Here, we investigate intraspecific sex ratio variation and its drivers in the Syntrichia ruralis-complex and in long-lived pleurocarpous mosses. We focus particularly on northern European populations of three mosses that occasional to rarely reproduce sexually and occur in different wetland habitats (Drepanoclados turgescens, D. trifarius, D. lycopodioides). In these, we identified sex based on sexual structures, when present, or used specifically designed molecular markers, when sex structures were absent, and calculated phenotypic and genotypic sex ratios.

In all studied species, reproductive females outnumbered reproductive males, sex expression levels and phenotypic sex ratios varied among regions, and they were partly related to sporophyte occurrences. Phenotypic and genotypic sex ratios of the Drepanoclados species were all female-skewed in the Scandinavian populations, and overall, there was no difference between the sexes in the proportions of sex expression. In D. turgescens, females were relatively more often sex expressing than males on the Baltic islands, but not on the Mainland. The genotypic sexes of D. trifarius were randomly distributed with respect to each other and to environmental conditions, suggesting absence of sexual niche partitioning at a Central Swedish site where the moss remains largely non-reproductive. In D. lycopodioides finally, wetness was negatively related to overall sex-expression and to genotypic sex ratio, i.e. relatively more genotypic females than males occurred in wetter places. This could be due to higher resource demands of females for sporophyte production, or higher male sensitivity to wet environments. Bryophyte sex response to environmental factors seems complex. We hypothesize that it depends on the species’ life history traits, including the level of sexual reproduction, general habitat, and their interactions, and it may thus vary among geographic regions and scales.

Max 5 words Keywords: Phenotypic and genotypic sex ratio variation, dioicous bryophytes, geographic scales, life history traits, environmental effects.
Intraspecific variation in heavy metal tolerance in two terrestrial moss species

M. Teresa Boquete1,2, Conchita Alonso1, Stuart F. McDaniel3, Sarah Carey3, Christina L. Richards4, Ingeborg Lang4, Irene Lichtscheidl5, Marieluise Weidinger5, Carlos Herrera1

1 Department of Ecology and Evolution of Plant-Animal Interactions, Estación Biológica de Doñana-CSIC, Sevilla, Spain (teresaboquete@ebd.csic.es); 2 Department of Integrative Biology, University of South Florida, Tampa, FL, USA; 3 Biology Department, University of Florida, Gainesville, FL, USA; 4 Department of Ecogenomics and Systems Biology, University of Vienna, Vienna, Austria; 5 Core Facility Cell Imaging and Ultrastructure Research, University of Vienna, Vienna, Austria.

Heavy metal (HM) toxicity constitutes a strong selective pressure that has led to ecotypic differentiation of many flowering plants in very short time frames. In bryophytes, there is still contrasting evidence about the relative contribution of population differentiation and phenotypic plasticity to adaptation to HM pollution, and limited information about the molecular pathways involved. In this study, we explored the molecular mechanisms underlying intraspecific variation in HM accumulation and tolerance in the Cu moss Scopelophila cataractae, and the cosmopolitan moss Ceratodon purpureus, two terrestrial moss species with contrasting affinity to HM. We sampled four populations of S. cataractae from different contamination levels within a former Cu mine, one population of C. purpureus in an urban area, and studied male and female plants of C. purpureus that were already growing in axenic lab conditions. We cultured all populations under control and Cu enriched conditions. To understand the response to this pollutant we measured Cu accumulation and plant performance (growth and oxidative damage), and used RNA sequencing to detect expression changes associated with HM exposure. Both species showed population-specific responses for tolerance, but Cu accumulation was similar in all populations within each species. S. cataractae isolates from the most polluted location in the mine were significantly more tolerant than the others. For C. purpureus, the field-collected population grew better than the lab-maintained population after Cu treatment. Gene expression profiles in control and Cu-treated plants revealed differential expression patterns in response to Cu in the two species. Furthermore, in C. purpureus, Cu-treated females had more differentially expressed transcripts (n=549) than Cu-treated males (n=4), when compared to control plants. These results provide evidence of significant population differentiation for HM tolerance at a very small spatial scale in S. cataractae, and of sex-specific molecular responses to Cu in C. purpureus.

Keywords: heavy metals, bryophytes, local adaptation, sexual dimorphism.
Bryophytes underground: diaspore banks in coastal dune systems

Des A. Callaghan¹, Heinjo J. During², Laura L. Forrest³, Karen Wilkinson⁴

¹Bryophyte Surveys Ltd, 65 Belle Vue Road, Stroud, Gloucestershire, GL5 1PY, UK (des.callaghan@bryophytesurveys.co.uk); ²Utrecht University, Netherlands (H.J.During@uu.nl); ³Royal Botanic Garden Edinburgh, Edinburgh, UK (LForrest@rbge.org.uk); ⁴Natural Resources Wales, Cardiff, UK (Karen.Wilkinson@cyfoethnaturiolcymru.gov.uk).

Hidden below ground, bryophyte diaspore banks remain very poorly understood and are usually ignored when undertaking conservation management activities. The purpose of this study is to investigate, for the first time, the occurrence and composition of diaspore banks in coastal dune systems. From eight sites in Wales (UK), 485 soil samples were collected from up to 30 cm depth and subject to germination trials in a growth chamber. Species that germinated were identified by morphological characters, supported by DNA barcoding. Bryophytes germinated from 291 samples (60%), mostly at shallow depth (<10 cm), represented by 35 species (7 liverworts and 28 mosses). Analysis of ecological attributes shows species in diaspore banks are significantly smaller in size, shorter lived and produce asexual propagules more frequently than species present aboveground. Of particular note, Amblyodon dealbatus, Red Listed in Wales, germinated from the diaspore bank of four sites, including a dune system where it was last seen in 1964 and considered extinct. The study highlights the fact that bryophyte diaspore banks comprise an important conservation resource that deserves careful consideration when planning management activities.

Keywords: conservation, diaspore banks, coastal dunes
Polyphyly of a common biocrust liverwort: *Riccia inflexa*.

D. Christine Cargill¹, Cécile Gueidan²

¹ Australian National Herbarium, GPO Box 1700. Canberra. 2601. ACT. Australia. (Chris.Cargill@environment.gov.au); ² Centre for Australian National Biodiversity Research, CSIRO. Canberra. 2601. ACT. Australia.

The genus *Riccia* is one of two genera which belong to the complex thalloid liverwort family Ricciaceae. *Riccia* is the most species rich with around 53 species described for Australia and approximately 200 species worldwide. They are most diverse in Mediterranean-type environments and are the most common liverwort species found in biological soil crusts. Polyphyly within a widespread and common southern Australian species of *Riccia* prompted a more detailed examination of this group which was usually placed under the species name *Riccia limbata* but more recently transferred to *Riccia inflexa*. In order to test this further, we sequenced collections identified as *R. inflexa* or *R. limbata* across a broad geographical range to determine relationships within the group. We also carefully re-examined the morphology of the group to uncover any overlooked vegetative and in particular spore characters that would support the phylogenetic relationships inferred from molecular data.

**Keywords:** Polyphyly, *Riccia limbata*, *Riccia inflexa*, biocrust, morphology, spore characters, molecular phylogeny
Predicting bryophyte species diversity in Canadian boreal forests using remote sensing data

Carlos Cerrejón, Osvaldo Valeria, Marion Barbé, Philippe Marchand and Nicole Fenton

Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada (carlos.cerrejonlozano@uqat.ca; osvaldo.valeria@uqat.ca; nicole.fenton@uqat.ca)

Bryophytes account for a significant fraction of biodiversity in boreal forests and play a crucial role in the functioning of these ecosystems. However, distribution and diversity patterns of bryophytes are poorly documented to date in Canadian boreal forests, hindering conservation tasks in the face of the high industrial activity in the region. The objective of this study was to develop predictive models and cartography of the total bryophyte richness as well as of the richness at the guild level (mosses, liverworts and sphagnum; four models in total) using remote sensing data. Our ultimate goal is to provide an ecological planning tool that allows identifying sites with a high ecological value to exclude them from the industrial development. The study area is located in western Quebec within the region Eeyou Istchee James Bay. A bryophyte presence/absence database from 326 plots was used to develop the response variable for each model, while Landsat spectral bands and indices, ALOS PALSAR data, and bioclimatic, topographic and soil-related variables were used as predictors. 70% of the data was used for model calibration and the remaining 30% for validation. Models and associated cartography were developed using the Random Forest algorithm in R. Resulting models explained 41.6 to 52% and 37.6 to 47.7% of the variation in the richness in the training and test datasets, respectively. Although in general spectral and bioclimatic variables appeared as the most important predictors of the richness of the different modeled groups, the best predictors as well as their relative importance varied among groups, which highlights the importance of working at the guild level to better identify the environmental parameters that determine the richness patterns of these species in relation to their ecological preferences and tolerances. While more accurate and reliable predictive models could be developed in the future using high-resolution data, the results of this study underline the potential of remote sensing in the field of predictive modeling of bryophyte biodiversity and lay the basis for eventual inclusion of bryophytes, until now overlooked, in ecological planning.

Keywords: boreal forests; bryophytes; predictive models and cartography; remote sensing; richness
Divergence and hybridization in the *Marchantia polymorpha* complex

Nils Cronberg¹, Anna-Malin Linde², Weerachon Sawangproh¹, Péter Szövényi ³, Ulf Lagercrantz²

¹ Department of Biology, Biodiversity, Lund University, Ecology Building, SE-223 62 Lund, Sweden (Nils.Cronberg@biol.lu.se, Weerachon.Sawangproh@biol.lu.se); ² Department of Plant Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden (anna-malin.linde@ebc.uu.se, ulf.lagercrantz@ebc.uu.se); ³ Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zurich, Switzerland (peter.szoevenyi@systbot.uzh.ch).

The potential role of hybridization and introgression in evolution has gained increased interest in recent years but more examples are needed to generalize its importance, especially concerning organisms with a dominant haploid generation, such as bryophytes. We analyzed genomes of three subspecies of the liverwort *Marchantia polymorpha*. We used available genomic data for subsp. *ruderalis* and carried out whole-genome (PacBio) sequencing for each one individual of subsp. *montivagans* and subsp. *polymorpha* as well as Illumina resequencing of additional genomes for all three subspecies. The three genomes were compared against *M. paleacea* as outgroup. Our analyses revealed separation of the three taxa, but all three possible topologies were richly represented across the genomes, and the underlying divergence order less obvious. This uncertainty could be the result of divergence of the three subspecies close in time, or that introgression has been frequent since divergence. In particular, we found that pseudo-chromosome 2 in subsp. *montivagans* was much more diverged than other parts of the genomes. This could either be explained by specific capture of chromosome 2 from an unknown related species through hybridization or by conservation of chromosome 2 despite intermittent or ongoing introgression, affecting more permeable parts of the genomes. A higher degree of chromosomal rearrangements on pseudo-chromosome 2 support the second hypothesis. Indications of recent hybridization were found in two populations. Species tree analyses recovered an overall topology where *M. polymorpha* *montivagans* diverged first and *M. polymorpha ruderalis* and *M. polymorpha polymorpha* appeared as sister species and each subspecies was associated with its own chloroplast and mitochondrial haplotype group. Our data suggest introgression but refute a previous hypothesis that subsp. *ruderalis* is a new stabilized hybrid between the other two subspecies.

Keywords: Incomplete lineage sorting, species complex, horizontal gene transfer, phylogeny, whole-genome sequencing
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Presentation type: Oral Presentation, Poster Presentation (underline the preferred type)

Where, when and what will be the effect of climate change on the distribution of *Anthoceros caucasicus* Steph.?

David Draper¹,²; Cesar Garcia¹; Manuela Sim-Sim¹,³; Cecília Sérgio¹

¹Museu Nacional de História Natural e da Ciência/CE3C- Centre for Ecology, Evolution and Environmental Change. Rua da Escola Politénica, 58, 1250-102 Lisboa, Portugal. email: ddmunt@gmail.com
²UBC Botanical Garden & Centre for Plant Research, and Department of Botany, University of British Columbia, Vancouver, Canada.

The effect of climate change on the species distribution will cause alterations of different sizes and magnitudes depending on the geographical zones and the characteristics of the species. The differentiated effect may be even greater when analyzing species that, although having a wide distribution, present great contrasts in the density of their populations. In this case, we analyze the changes in quantity and quality of the habitat of *Anthoceros caucasicus* Steph. throughout its distribution using ecological niche models. The aim is to evaluate current conditions and how may change in the near future. We used the Maxent algorithm and five global circulation models under three scenarios proposed by the IPCC. We evaluated decade to decade between 2020 and 2080 for the temporal space projection. Results obtained show a considerable increase in the quality of the habitat in Macaronesia as in the regions of the Atlantic cornice (mainly at Macaronesia bioregion, mainland Portugal and Ireland), the Balkan region, Tunisia and the east coast of the Mediterranean are also shown as areas where the species can reach its habitat in the immediate future. The current Caucasian and Italian population will be negatively affected due to a decrease of habitat availability and habitat quality. *Anthoceros caucasicus* distribution is not compromised in general terms, although large variations are expected on a local scale that could jeopardize the genetic flow (if it still exists) between the east and west Mediterranean populations.

Keywords: *Anthoceros caucasicus*, habitat quality, ecological niche models, Macaronesia, Mediterranean.
A new insight into the genus *Pulvigera* (Orthotrichaceae) in North America

Draper, I.1,2, Lara, F.1,2, Flagmeier, M.1, Calleja, J.A.1, Mazimpaka, V.1,2 & Garilleti, R.3

1 Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid, c/ Darwin, 2. E-28049, Madrid. isabel.draper@uam.es; francisco.lara@uam.es; maren.flagmeier@uam.es; juan.calleja@gmail.com; vicente.mazimpaka@uam.es; 2 Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), c/ Darwin, 2. E-28049, Madrid; 3 Departamento de Botánica y Geología, Facultad de Farmacia, Universidad de Valencia, Avda. Vicente Andrés Estellés s/n. E-46100, Burjassot. ricardo.garilleti@uv.es.

*Pulvigera lyellii* (Hook. & Taylor) Plášek, Sawicki & Ochyra (≡ *Orthotrichum lyellii* Hook. & Taylor) is considered a moss morphologically variable to some extent, especially in North America, and currently includes several synonyms. In this study, we have analyzed its morphological and genetic variation within an integrative taxonomy framework. We have combined morphological and biogeographical pieces of evidence with a phylogenetic reconstruction based on five molecular markers from both the nuclear (ITS2 and one unpublished region) and the chloroplast (trnG, trnLF and rps4 loci) genomes. The detailed study of a considerable number of specimens (over 100 samples in the case of the morphological analyses) reveals solid and constant morphological differences, which are strongly supported by the genetic variability. We conclude that the current concept of *Pulvigera lyellii* comprises no less than four distinct entities at species level. Thus, our results notably increase the recognized diversity in the genus *Pulvigera* Plášek, Sawicki & Ochyra, and refute its so far consideration as a monospecific character. The four species include *Pulvigera lyellii* s.s., plus three other taxa formerly described but are at present treated as synonyms of *P. lyellii*. Based both on our morphological and genetic results, we propose the reinstatement of these three taxa at the level of species, and we provide the main morphological traits to distinguish them.

Keywords: Orthotricheae – *Orthotrichum lyellii* –*Pulvigera lyellii* – Taxonomy – North America
The recent revisions of moss taxa of the Moss Flora of Russia with integrative taxonomy approach found a number of similar phytogeographical patterns. European species traditionally assumed as circum-Holarctic or at least Eurasian in distribution appeared to be confined to Europe, having eastern boundary of distribution within the European Russia. Examples are provided by *Rhynchostegium riparioides*, *Polytrichum formosum*, *Schistidium apocarpum*, *Lewinskya speciosa*, *Ulota crispa*, *Hedwigia ciliata*, *Plagiothecium laetum*. Eastern vicariants may be well segregated geographically (*Polytrichum formosum/ P. densifolium, Hedwigia ciliata /H. mollis, Rhynchostegium riparioides / R. aquaticum s.l.*) or have a considerable overlap, e.g. *Lewinskya speciosa/L. elegans*. Interestingly haplotypes of *Neckera pennata* complex often have coincident geographical limits: amphiatlantic, two amphipacific, circumboreal, South Chinese and two montane; among them only saxicolous *N. oligocarpa* has stable morphological differences and presumably may represent suite of cryptic or semi-cryptic species. Highly supported infraspecific groupings corresponding to geographical patterns were found in course of our molecular phylogenetic studies also in widespread species of *Anomodon*, Rhabdoweisiaceae, *Amphidium*. Thus, the overall diversity of mosses within the circumboreal region turns to be much higher than it was though before. Among found bryogeographical boundaries the western administrative border of the former USSR and boundary of the permafrost territory in continental climate of Asia seems are more prominent that thought earlier. The work was supported by RSF 18-14-00121.

Keywords: integrative taxonomy, hidden diversity, biogeography
Mosses are amongst the simplest and oldest plants on Earth. Despite their small size, they played a remarkable role shaping our planet. Still in our era, they are one of the largest groups of land plants and can be found almost everywhere in the world, and they continue to condition the structure and function of ecosystems. Their simplicity and particular physiology make bryophytes interesting subjects of study in ecology, especially because the lack of cuticles makes them extremely sensitive to environmental changes. Nonetheless, the proportion of ecological studies focused on bryophytes is clearly insufficient despite the fact that knowing bryophytes better could provide important insights about unresolved questions of physiology and the ancient evolution of plants. We have investigated aquatic and semi-aquatic (hygrophytic) mosses growing in semi-natural Mediterranean springs. These springs pour water continuously throughout the year, which makes them behave like small islands, or refugia, where water is available, surrounded by completely different habitats where water is scarce. Here, we analysed water chemical composition and moss communities of 303 semi-natural springs around NE Iberian Peninsula and investigated the relationship between 12 moss functional traits and the environment. Our results indicated phylogenetic conservation of several moss functional traits, and that, most likely, water conductivity acted like an environmental filter. Moss size and spore size were also related to water properties and climate. Hence, our results indicate that moss assemblages in semi-natural springs can be determined by water chemistry, highlighting the role of elements in shaping moss distribution.

Keywords: Semi-natural springs, morphology, water conductivity, carbonate crusts, hygrophytic
Northern and mountain bryodiversity must be better understood when the climate gets warmer

Lars Hedenäs
Department of Botany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

The effects of the gradually warmer climate on organisms and their diversity will be especially strong in mountains and, in the Northern Hemisphere, towards the north. We are likely losing intraspecific genetic diversity faster than diversity related to rare species. From a biodiversity conservation point of view, it is therefore crucial to know more about the frequency of northern and mountain genetic variants in widespread bryophyte species. This investigation examines diversity patterns and the occurrence and distribution of northern and mountain genetic variants in ten widespread mosses in Sweden, a country that extends from the nemoral to northern portion of the northern boreal zone and includes 12.5% alpine and subalpine areas. Between 50-110 specimens were sampled per species, from herbarium S or collected in the field, with the densest sampling in the north. For each species, (2-)3(-4) molecular markers were used to explore haplotype diversity and patterns of genetic relationships, based on NeighborNet split networks and Jacknife analysis. Eight of the ten species include lineages or groups of haplotypes that occur exclusively in the north or in the mountains. However, also in the two species lacking such lineages or groups, the genetic composition differs (population pairwise ΦPT, or corrected average number of pairwise nucleotide differences) between the north or the mountains on the one hand, and the south or the lowlands on the other. In some of the studied species, the genetic variation is correlated with morphology, which could indicate so-far unrecognized species, whereas in other species no morphological differentiation exists. The geographical distributions of northern or mountain genetic variants coincide with those regions of northern Sweden that will be most strongly affected by the expected future warming; examples of potential climate effects among the studied species are provided. The results of this study show that we will likely lose significant portions of our intraspecific biodiversity in the north, even if the species themselves, as currently circumscribed, will probably survive ‘without problems’.

Keywords: climate change, habitat loss, intraspecific diversity, northern or mountain genetic variants
Predicting bryophytes’ vulnerability to climate change: combination of niche and spatial metrics matter!

Helena Hespanhol¹, Katia Cezón², Jesús Muñoz², Rubén G. Mateo³,⁴, João Gonçalves¹

¹CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto, Campus Agrário de Vairão, R. Padre Armando Quintas, 4485-661 Vairão, Portugal (helenahespanhol@cibio.up.pt); ²Real Jardín Botánico (CSIC), Plaza de Murillo 2, 28014 Madrid, Spain; ³Department of Biology (Botany), Universidad Autónoma de Madrid, C/ Darwin 2, ES-28049, Madrid, Spain; ⁴Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, 28049, Madrid, Spain.

Range contractions have been predicted for numerous European bryophyte species, as well as range expansions for others at their northern limits. It has been hypothesized that species with different distributions in environmental niche and geographical space may respond differently to changes in climate. The aim of this study is to assess how niche and spatial metrics are related to bryophytes’ vulnerability to climate change.

We used a dataset on mountain saxicolous bryophyte species in Iberian Peninsula that are likely to be most vulnerable to the impacts of climate change. The current and future distribution for 39 bryophyte species were predicted by species distribution models using climatic and topographic variables known to have an important role in limiting such plants. Niche metrics, specifically niche breadth, niche position and niche overlap, were calculated using a new tool based on multidimensional kernel density estimation procedure. The same and corresponding metrics that were used to characterize the environmental space were calculated for the geographic space. Future projections for the year 2050 were derived using two different Global Climate Models recommended for Europe and Mediterranean climates. Species range changes, specifically range contraction, were then related to niche and spatial metrics using linear regressions.

Correlation results between species range contractions and niche and spatial metrics revealed that bryophyte species with higher marginality, narrow niche breadth and restricted range are more likely to experience range contractions. Taking in account different climate change scenarios in 2050, the best models explaining bryophytes’ range contractions included the single effect and combination of niche metrics (breadth and position) and also the combination of range size and niche metrics (breadth and position).

Our results suggest that the combination of niche and spatial metrics may improve predictions about bryophytes’ vulnerability in the context of global changes.

Keywords: niche breadth; niche position; range size; range contraction; ecological modelling
Dissecting the genetic basis of seasonal reproduction in a basal land plant, the moss *Physcomitrella patens*

Karen A. Hicks¹, Viktoriya Coneva¹, Keith Adler¹, Kiersten Bell¹, Kristen Edgeworth¹, Jonathan Flowers², Alex Freidinger¹, Hannah Hertz¹, Katherine Lang¹, Carter Powell¹, Shawn Ruiz¹, Maria Sorkin¹

¹ Biology Department, Kenyon College, 202 N. College Rd., Gambier, OH 43022, U.S.A. (hicksk@kenyon.edu); ² Center for Genomics and Systems Biology, New York University, 12 Waverly Place, New York, NY 10003, U.S.A.

Many plants make use of environmental cues, such as daylength and temperature, to synchronize reproductive development with favorable climatic conditions, thereby increasing their reproductive success. Although the genetic mechanisms that regulate reproductive development in response to seasonal cues are largely conserved across flowering plants, it is not known whether this conservation extends beyond angiosperms to other land plant lineages. We are using the model moss *Physcomitrella patens* to probe the evolutionary origin of seasonal regulation in land plants, with the long-term goal of determining whether a core mechanism evolved in the common ancestor of all land plants, or if convergent mechanisms arose separately in distinct land plant lineages. We are coupling transcriptomic and genomic analyses of a set of *P. patens* ecotypes that vary in reproductive timing in response to seasonal cues with traditional mutagenesis screens to identify and characterize the genetic networks that underpin seasonal regulation of sexual reproduction in this basal land plant. Using a combination of cross-population genome-wide measures of selection and differential co-expression network analysis comparing ecotypes across daylength and temperature conditions, we have narrowed in on candidate genes homologous to upstream components of angiosperm temperature and daylength induced flowering time pathways. We have generated CRISPR-Cas9 mutants in four gene families and are currently evaluating their phenotypes. In parallel, we designed a mutagenesis screen, which has yielded heritable mutants with striking differences in the timing of onset of reproductive development in response to seasonal cues.

Keywords: Sexual reproduction, seasonal regulation, natural variation, transcriptomics, CRISPR-Cas9
Information for submission of abstracts to the Bryology 2019 meeting. Deadline: 31 May 2019

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A new bryophyte Red List and Checklist for Europe

N.G. Hodgetts

Affiliations¹, (email of presenting/corresponding author is required; other emails are optional, but recommended) nick1901@hotmail.co.uk

A new European Red List for bryophytes is being published. This is a collaborative project between the European Committee for the Conservation of Bryophytes (ECCB), the Species Survival Commission (SSC) Bryophyte Specialist Group and the International Union for the Conservation of Nature (IUCN), with support from the EC LIFE fund. To accomplish this task – the assessment of 1,817 species occurring in Europe – more than 100 bryologists have been working on this list over the last 3 years. The system used for species assessment follows the IUCN methodology but critical terms (e.g. generation length) had to be interpreted to become applicable for bryophytes. 22.5% of the European bryophyte flora is threatened (VU, EN, or CR), although only 6 species are considered Extinct (EX) or Regionally Extinct (RE). Mountainous regions, especially the Alps, are particularly rich in threatened species; hyperoceanic areas are particularly rich in endemic and near-endemic species. Major threats to European bryophytes include natural system modifications, including forestry and agricultural intensification, and climate change. Concurrently, a new European bryophyte Checklist is being prepared. This will include a published checklist and also a spreadsheet showing the distribution of species by country throughout Europe. It is intended that both projects will contribute to future research into bryophytes in Europe, and particularly provide a tool for their conservation.

Keywords: bryophytes, conservation, Red List, checklist, Europe
The Pyrenean bryoflora: erasing national borders in the FLORAPYR Atlas

Marta Infante1,2, Patxi Heras2,3, Montserrat Brugués4, Vincent Hugonnot5, David G. Long6, Benoît Offerhaus7, Gordon Rothero8, Elena Ruiz4

1 Conservatoire botanique national des Pyrénées et de Midi-Pyrénées (CBNPMP), Bagnères-de-Bigorre, France (marta.infante-sanchez@cbnpmp.fr); 2 Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; 3 Bazzania S.C., Investigación y Gestión en Biodiversidad, Vitoria-Gasteiz, Spain (bazzania@arrakis.es); 4 Universitat Autònoma de Barcelona, Spain; 5 Blassac, France; 6 Royal Botanic Garden, Edinburgh U.K.; 7 Conservatoire botanique national Méditerranéen, France; 8 Dunoon, Argyll, U.K.

In southwestern Europe, the Pyrenean range extends 440 km from West to East, 30 – 150 km from North to South, in latitude 42 – 43.3° N. Its highest point is Aneto summit (3.404 m), but it contains more than a hundred peaks over 3.000 m, and therefore stands out from the other mountain ranges in Southern Europe, excepting the Alps. Its 44.000 km² extend over three countries (France, Spain and Andorra); constituting the limit between two large bioclimatic regions, the temperate and the mediterranean.

A first global bibliographic checklist in 2013 compiled data from more than 700 publications spanning over 230 years, so gathering the contribution of over 250 authors, and yielded 1.069 taxa, 60% from 1.780 estimated for Europe, 73% of the bryophytes reported for metropolitan France and 89% of those reported for peninsular Spain.

The online resource Atlas of the Flora of the Pyrenees was developed for vascular plants in the POCTEFA 2007-13 OPCC project (Interreg European Union). The new POCTEFA 2014-20, FLORAPYR Project now includes the bryophytes in this Atlas; compiling bibliographic, herbarium and observational data from six institutions and main collaborators, and drafting a factsheet for each taxon which includes a distribution map, a biological file with different sections, and images.

The updated (but still evolving) list now includes 1069 taxa at species level, amounting to 1121 taxa at infraspecific level. These species are distributed in 4 anthocerotes, 266 liverworts and 799 mosses. The strong dissymmetry north-south is barely reflected in global species figures, but distribution types for the different elements (arctic-alpine, atlantic or mediterranean) are becoming evident.

The Pyrenees are shown to be an area of extraordinary bryological richness. This cross-border collaborative effort being made will in future provide a solid basis for conservation action on a total Pyrenean scale.

Keywords: European bryophytes, Pyrenees Mountains, atlas, cartography
One Mountain, Two Slopes – Heterogeneity of epiphytic bryophytes communities on Mt. Gede

Eka A.P. Iskandar¹²³, Michael Stech¹², Sylvia Mota de Oliveira¹²
¹Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands (eka.iskandar@naturalis.nl); ²Leiden University, Leiden, The Netherlands; ³Cibodas Botanic Garden – Indonesian Institute of Sciences (LIPI), Cibodas, Indonesia.

Variations among bryophyte communities along elevational gradients in the tropics have been reported in several studies. However, not much information is available on the epiphytic bryophyte species richness pattern, composition, and zonation in South-East Asia. This study aims to compare the bryophyte species richness pattern, composition, and zonation between two slope aspects of Mt. Gede, West Java, Indonesia. One elevational gradient transect was established on the drier North-North-East (Cibodas) slope and another one on the wetter South-South-West (Selabintana). Both transects range from 1500 to 2700 m asl., and epiphytic bryophytes were sampled at 200 m intervals. Our study finds that the Cibodas transect is richer (160 species; 71 mosses and 89 liverworts) than the Selabintana transect (149 species; 57 mosses and 92 liverworts), probably due to topographic variations. Species richness pattern on both slopes showed quadratic responses for mosses and cubic responses for liverworts. Lejeuneaceae, Lepidoziaceae, and Plagiochilaceae were the most common families on both transects. Statistical analyses on species composition showed five significantly different zones – Submontane, Lower Montane, Transition, Upper Montane, Subalpine – on each slope aspect, with wider Lower Montane zone on Selabintana and Subalpine zone on Cibodas. A distinct transition zone was present between Lower and Upper Montane zone on both slope aspects, which was not reported in previous bryophyte studies. Every zone has its own indicator species, except for Upper Montane zone on Selabintana. No indicator species were shared among zones of Cibodas and Selabintana, except for Syrrhopodon tristichus at Lower Montane zone. The present study contributes to a better understanding of bryophytes communities in tropical mountainous areas.

Keywords: elevational gradient, species richness pattern, zonation, mosses, liverworts
Male dwarfism is uniquely found in unisexual mosses. It is a strategy that brings males and females close together, thereby facilitating sexual reproduction. Hence, dwarf males could significantly contribute to the gene pool transmitted to the next generation through the sporophytes. However, a dwarf male breeding system can also lead to complete homozygotization after only a few generations if repeated mother-son fertilization occurs. In the widespread moss species *Dicranum scoparium* Hedw., the female gametophore is always normal-sized, whereas males are facultatively nannandrous. This means that male individuals can either be normal-sized and free-living (“NMs”) or dwarfed and attached to females (“DMs”). We analysed the spatial distribution of female and male haplotypes to assess the influence of this mixed breeding system on genetic variability, population structure and clonality. We used 119 SNPs to genotype plant material from 11 sites in seven localities in southern Sweden. A total of 403 individuals were analysed (211 females, 135 DMs and 57 NMs). DMs and NMs were encountered in all localities but one for NMs. If NMs were much less frequent than DMs, the exact female:male ratio is difficult to assess. Nevertheless, our overall ramet- and genet-level data suggest a rough female:NM estimate of 4:1 respectively 3.5:1, which is comparable to what was found in other species such as in *Mnium hornum, Bryum argenteum*. AMOVAs (analysis of molecular variance) indicated a low differentiation at site and locality levels while most of the variance was found between cushions for females and NMs and within cushions for DMs. Haplotypes were sometimes shared among individuals of the same sex, suggesting clonal propagation. Dwarf males had mostly one haplotype per individual and were genetically more diverse than the two other groups. We also found two haplotypes that were shared between females and DMs and one haplotype that was shared between a DM and a NM. The results suggest effective and frequent gene flow between populations, even over long distances, via male spore dispersal. Demes are often genetically diverse, but we also see indications of inbreeding, probably caused by repeated mother-son fertilizations.

Keywords: facultative dwarfism, spore dispersal, genetic variation, sexual reproduction
The acrocarp moss *Atrichum undulatum* tolerates pollution of copper and zinc depending on environmental conditions

Ingeborg Lang¹, Marieluise Weidinger², Aneta D. Sabovljevic³, Jelena Stankovic³, Wolfram Adlassnig² and Marko S. Sabovljevic³

¹Department of Ecogenomics and Systems Biology, Faculty of Life Sciences, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria
²Cell Imaging and Ultrastructure Research, Faculty of Life Sciences, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria
³Instutute of Botany and Botanical Garden, Faculty of Biology, University of Belgrade, Takovska 43, 11000 Belgrade, Serbia

Mosses are frequently used to monitor atmospheric metal contamination but few studies focus on the mechanisms of metal adsorption under controlled conditions. Here, we studied the accumulation of the heavy metals copper and zinc in the acrocarp moss *Atrichum undulatum*, which has been frequently used in biomonitoring. An in vitro culture of *A. undulatum* was established and the same line, size and equally old remets were exposed to six different treatments representing various metal exposure times and washing scenarios as rain simulation. The metal treatments were done in two concentrations of copper and zinc salts (Cu-acetate, CuSO₄, ZnSO₄ and ZnCl₂, respectively). Energy-Dispersive X-ray microanalysis (EDX) was employed to detect bound heavy metals on the moss plantlets. Element distribution in stems and leaves was measured separately. The results clearly showed that *A. undulatum* is tolerant to contaminations with zinc and copper, and that zinc is less toxic and less bound to the plant than copper. An aqueous solution of metal salts facilitated an adsorption of both elements in the moss tissue as compared to solid medium. Furthermore, *A. undulatum* tolerated pollutions of zinc and copper in a distinctive extent; our data point towards a zinc tolerant species whereas copper is rather harmful. Interestingly, a strong positive correlation between the accumulation of copper/zinc and iron, and a strong negative correlation between copper/zinc and magnesium, respectively, was documented.

Keywords: bryophyte, toxic, accumulation, heavy metal, rain simulation
An interesting distribution pattern of most liverworts shows that they are of ancient Cretaceous origin and their diversification started in the Cenozoic. For example, in the most species-rich family of liverworts, Lejeuneaceae, divergence-times estimation indicates a rapid establishment of the major lineages in the Cretaceous followed by steady diversification through the Cenozoic. Here we aimed at investigating the historical biogeography of the subcosmopolitan genus *Lejeunea* (Lejeuneaceae) based on phylogenetic analyses and to explore how the genus achieved its subcosmopolitan distribution. Relying on a taxon sampling that covers approximately the full geographical distribution, we used macroevolutionary analyses to estimate the ancestral areas of origin and assess whether palaeoenvironmental changes and sexual system influenced the species diversification of *Lejeunea*. Maximum likelihood and Bayesian inference were used for phylogenetic analyses using sequences of two chloroplast regions and one nuclear region. Divergence times were estimated using a Bayesian molecular relaxed-clock constrained with fossil calibrations. Diversification rate analyses were carried out under time-dependent, environmental-dependent, and trait-dependent models. Ancestral areas were reconstructed with likelihood-based methods using the Dispersal-Extinction-Cladogenesis model. *Lejeunea* diverged from its sister group at the Paleocene-Eocene boundary (56.7 Ma, 95% credibility interval: 46.3-63.8) and the initial diversification of the crown group occurred in the early to middle Eocene (47.5 Ma, 95% credibility interval: 37.6-54.7). *Lejeunea* is most likely to have originated in the Neotropics, however, the “out of North America” hypothesis cannot be ruled out. The evolutionary history of *Lejeunea* shows several biogeographic scenarios in shaping the global distribution of the genus. The unusual northern routes of colonization through the Bering land bridge may have facilitated the dispersal from North America to Continental Asia at least twice during the Oligocene and late Miocene. The Miocene was an important period for *Lejeunea* when they diversified globally. Monoicy is associated with higher diversification rates in *Lejeunea* lineages while past temperature did not influence the diversification of *Lejeunea*. Moreover, the results point to the constant accumulation of diversity through time in *Lejeunea*, in line with the previous evidence in Lejeuneaceae, which underwent a steady diversification through the Cenozoic.

**Keywords**: Subcosmopolitan, historical biogeography, Bering land bridges migration, Miocene diversification, *Lejeunea*
Study of cryptic peptides biological activity in plants

Irina Lyapina¹, Anna Filippova¹, Ilya Kirov², Ekaterina Grafskaia³, Vasily Lazarev³, Victor Zgoda⁴, Igor Fesenko¹

¹ Laboratory of functional genomics and plant proteomics, Institute of bioorganic chemistry RAS, Moscow, IN 117997, Russia (amadeynemez@gmail.com); ² Laboratory of marker and genomic plant breeding, All-Russia Research Institute of Agricultural Biotechnology, Moscow, IN 127550, Russia; ³ Laboratory of gene engineering, Federal Research and Clinical Centre of Physical-Chemical Medicine, Moscow, IN 119435, Russia; ⁴ Laboratory of System Biology, Institute of Biomedical Chemistry, Moscow, IN 119121, Russia.

Despite the lack of an adaptive immune system, plants have a complex innate immune system that has developed during the process of co-evolution of plants and microorganisms. Cell wall receptors, such as receptor-like kinases, recognize conservative molecular patterns of pathogens (PAMPs) as well as host damage associated molecular patterns (DAMPs). PAMPs and DAMPs are often peptides - fragments of functional or non-functional precursor proteins. Recent studies have shown that plant endogenous peptides, such as PEP, are able to activate the expression of defense genes, thereby regulating the immune response of plants. The role of cryptic peptides encoded in the functional protein sequences of both plants and pathogens has been little studied. Such peptides can have both signaling and antimicrobial activities.

For the discovery of new functional cryptic peptides, the intracellular and secreted peptide pools of a model plant, moss Physcomitrella patens, were analyzed during the treatment with stress hormones salicylic acid (SA) and methyl jasmonate (MeJA). An analysis of the mass spectrometry data revealed a number of peptides unique to the treated samples, among which potential candidates for bioactive peptides were identified. We have shown that treatment with hormones led to an increase in the antimicrobial activity of the extracellular peptide, and an addition cocktail of protease inhibitors, on the contrary, reduced it, which may indicate the role of proteases in the formation of the bioactive peptide pool. Using bioinformatics methods, we predicted proteases that respond to stressful conditions. In addition, we have shown the effect of SA treatment on the proteasomal activity inside the cells, which is obviously involved in the change in peptide pools. We also synthesized eight peptides with predicted antimicrobial activity. We showed that a peptide INIINAPLQGFKIA derived from predicted protein precursor inhibited bacterial growth in 16 μg/ml concentration and influenced the transcription of defense genes.

Keywords: Physcomitrella patens, peptidomics, plant immunity, LC-MS/MS
**Presentation type:** Oral Presentation, Poster Presentation

**Which climatic and environmental factors determine liverwort diversity patterns in tropical montane forests?**

Karola Maul, Yu-Mei Wei, Boon-Chuan Ho, Martin Nebel, Federico Luebert, Michael Kessler, Dietmar Quandt

1 Nees-Institute for Biodiversity of Plants, University of Bonn, 53111 Bonn, Germany (Karola.maul@uni-bonn.de); 2 Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and the Chinese Academy of Sciences, Guilin, Guangxi 541006, China; 3 Herbarium of the Singapore Botanic Gardens, 1 Cluny Road, Singapore 259569, Singapore; 4 Institute of Systematic Botany, University of Zurich, Zollikerstraße 107, 8008 Zürich, Switzerland.

Global biodiversity is not equally distributed. Typically, species richness declines with increasing latitude from the equator towards the poles. Also on regional and local scales, the distribution of biodiversity is heterogenous: along elevational gradients, many organisms, including early diverging land plants, show a hump-shaped pattern, peaking at middle elevations. The knowledge about the mechanisms and processes determining this pattern have not yet been fully elucidated. The aim of this study was to examine the species richness distribution patterns and the underlying causes of liverworts along an altitudinal gradient in the tropics. We surveyed the species richness of epiphytic and non-epiphytic liverworts in 24 plots in mountain forests at 680-3200 m above sea level in Uganda. A total of 120 liverwort species and subspecies from 18 families were identified. Generalized linear models (glm) were calculated to assess the impact of climatic and environmental factors on species diversity. Our results provide evidence for different altitudinal maxima of species richness in epiphytes (1800 m) and non-epiphytes (2200 m). The predicted species richness also shows a hump-shaped pattern when contrasted against mean annual temperature, and against annual precipitation peaking at around 17 °C, and 1450 mm, respectively. Our data also suggest that species diversity in liverworts increases with increasing precipitation in the dry season, and decrease in diversity with increasing habitat homogeneity. Epiphytic and non-epiphytic species seem to have different preferences regarding precipitation, temperature and cloud cover.

**Keywords:** species richness distribution, elevational gradient, tropical montane forest, climatic conditions
Liverworts are among the most common epiphylls on leaves in tropical rainforests. Due to their fast life cycle and the great replication of well-delineated communities, epiphyllous liverworts, together with algae, fungi, and lichens, represent a promising model to test ecological theories about biodiversity maintenance and community development. The aim of this study is to understand how neighbor interactions shape epiphyllous liverwort communities and how these interactions differ between closed-forest and gaps. To this end, we characterized the spatial structure of epiphyll communities on ten leaves each in gaps and closed-forest over time, resampling at four-time intervals (at 0, 6, 9 and 12 months). For analysis, epiphylls were divided into four functional groups: liverworts, algae, fungi and lichens. We analyzed the spatial and temporal structure of epiphyll communities using point-pattern analysis, assuming that spatial aggregation indicates positive interactions and segregation indicates negative interactions, while random patterns indicate chance processes being dominant. We found that with time, more leaves started to show aggregated rather than random patterns in liverwort distribution. Spatial associations between liverworts and other epiphylls were mostly positive or random on young leaves, but became negative on some of the aging leaves. The more random patterns on young leaves probably indicate that the pattern is determined mostly by chance arrival of propagules. On older leaves, aggregation may indicate local dispersal or facilitation. Interspecific negative associations on aging leaves may point at competition for space between these functional groups. Epiphyll communities were shown to be highly dynamic, with spatial patterns and interactions changing during community development, from random to interactive.

Keywords: epiphylls, interactions, liverworts
Life on earth depends on photosynthetic organisms capable of exploiting sunlight to fuel synthesis of ATP and reducing power. Natural environmental conditions are highly variable and photosynthetic electron transport requires continuous modulation to maintain the balance between light availability and metabolic demands. Photosynthetic organisms evolved multiple mechanisms to modulate the flow of excitation energy and electrons according to metabolic constraints and environmental cues.

Even if photosynthesis is finely regulated in all organisms, the molecular mechanisms are generally not conserved and different phylogenetic groups show significant differences. In the past few years we investigated how mechanisms for regulation of photosynthetic electron transport adapted during land colonization, using the moss *Physcomitrella patens* as a model. As example, we showed that Flavodiiron proteins (FLVs) have a major role in *P. patens* response to light fluctuations but FLV-encoding sequences were nevertheless lost during evolution by Angiosperms, suggesting that their activity become superfluous or even detrimental for photosynthetic efficiency in those species.

By generating *P. patens* KO plants depleted in regulatory electron transport mechanisms, we also demonstrated that different mechanisms for electron transport regulation have strong functional overlap and, when one is depleted, the others can compensate for the activity. When multiple mechanisms are simultaneously inactivated, however, plants showed major reduction in growth, demonstrating that photosynthesis cannot work efficiently without regulation.

**Keywords:** metabolism, response to environment, light response,
**Presentation type:** Oral Presentation, Poster Presentation

**Climate change effects on the carbon balance of tropical lowland bryophytes**

Nikolic Nada\textsuperscript{1}, Elodie Moureau\textsuperscript{1}, Gerhard Zotz\textsuperscript{2} & Maaike Y. Bader\textsuperscript{1}

\textsuperscript{1} Philipps-Universität Marburg, Faculty of Geography, Ecological Plant Geography (nada.nikolic@geo.uni-marburg.de, elodie.moureau@geo.uni-marburg.de, maaike.bader@uni-marburg.de)

\textsuperscript{2} University of Oldenburg, Institute for Biology and Environmental Sciences, Functional Ecology of Plants (gerhard.zotz@uni-oldenburg.de)

Different effects of climate change have already been recorded and the future might be too hot for some organisms, especially in the tropics. Bryophytes in tropical lowlands have low abundance even under current conditions and may suffer if their climate warms further. Possible reasons for negative warming effects are increased rates of night respiration that are hard to compensate by short photosynthetic activity (due to faster drying) and/or low photosynthetic rates (due to low light in the forest understorey). We therefore study how carbon balances of tropical bryophytes may change with changes in climate by modelling long-term carbon balances based on microclimatic conditions. As a study case we use selected understory epiphytic bryophytes from the tropical lowlands of Costa Rica, for which we also simulated climate change in open-top chambers in an \textit{in situ} experiment. Photosynthetic responses to different light, temperature, CO\textsubscript{2} concentration and water content were measured using an infra-red gas analyser. These response curves were used to parameterise the carbon module of our model. The hydration module (calculating water content depending on temperature and relative humidity) is based on empirical measurements of bryophyte drying speeds. With this model we simulated warming effects on photosynthetic rates and/or on drying. Even with a moderate increase of temperature of 3K, modelled carbon balances show significant decreases, although these depend on weather conditions. Increasing atmospheric CO\textsubscript{2} partly compensated for this negative effect in the model, but in the \textit{in situ} experiment increased CO\textsubscript{2} did not increase the performance of the bryophytes, which suffered from warming. By combining modelling with experimental results, we will present possible future carbon balances of tropical lowland bryophytes. With further development of the model, it could also be used to predict biogeographical distributions of bryophytes.

**Keywords:** tropical lowland bryophytes, carbon balance, modelling, ecophysiological response curves,
Biocontrol Potential of Himalayan Bryophytes against different microorganisms

Kavita Negi¹, Preeti Chaturvedi²

¹Central Council for Research for Unani Medicine (Ministry of Ayush), OPP-D-Block, Janakpuri, New Delhi-110 058 INDIA (negikavita123@gmail.com); ²Department of Biological Sciences, C.B.S.H., G.B. Pant University of Agriculture & Technology, Pantnagar 263145, Uttarakhand, INDIA.

Most of the natural plants products that are in use worldwide are obtained from angiosperms. Lower group of plants like bryophytes are relatively unexplored and underutilized worldwide. In the present study, the acetone and ethanol/methanol (80%) extracts of nine bryophyte species (liverworts and mosses) collected from different altitudes of Kumaon, Himalaya (INDIA) were investigated for their antimicrobial potential against different bacteria and fungi using disc diffusion assay. The minimum inhibitory concentration (MIC) and minimum bactericidal or fungicidal concentration (MBC/MFC) was observed employing micro broth dilution methods. Lowest MIC and MBC/MFC (0.97 to 125µg/mL) was found in methanolic extract of Conocephalum conicum (liverwort) against bacteria (Salmonella enterica, Erwinia chrysanthemi, Pseudomonas aeruginosa) and fungi (Colletotrichum falcatum, Aspergillus sp., Fusarium oxysporum f. sp. lycopersici). Further, in vivo study through green house experiments confirmed the potential of C. conicum as an efficient biofungicide to control fusarium wilt disease in tomato. Scanning electron microscopic studies also helped in confirmation of biocontrol potential of C. conicum to control Aspergillus sp.

Biochemical profiling of the methanolic extract of C. conicum was done through antioxidant (phenol, flavonoids) and GC-MS analysis. Out of 18 different organic extracts, methanol extract of C. conicum was found most potent showed highest antioxidant activity (90.17±1.63%). In GC-MS analysis, riccardin C, a biomarker compound along with sesquiterpenoids (citronellol, trans-Squalene, geranylgeraniol, lactone G), phytol and steroids were detected in C. conicum. Future optimization of these bioactive compounds may emphasize upon their potential role in its application in the development of novel antimicrobial agents.

Keywords: Bryophytes, antimicrobial activity, SEM, antioxidants, GC-MS.
Exploration of the Southeast European bryophyte flora with a special attention to the species of conservation interest

Beata Papp¹
¹Hungarian Natural History Museum, Botanical Department, H-1431, Budapest, P.O.B. 137, Hungary, papp.beata@nhmus.hu

In the last 20 years the Bryological Collection of the Hungarian Natural History Museum (HNHM) has dealt intensively with the Balkan Peninsula, from where there is still relatively few data compared to other parts of Europe. Several joint field trips with SE European bryologists were organized. Special attention was paid to the investigation of the habitats of rare, threatened species. As a result more than 18,000 specimens have been deposited in the HNHM and 87 papers have been published. Voucher specimens of 619 species can also be found in HNHM, which were reported for the first time from the various countries of Balkan. From conservation point of view wetlands are the most important habitat types in SE Europe, threatened mainly due to climate warming. Their extension is decreasing, and they are continuously losing the sensitive bryophytes of their species pool. Although the suitable bogs are small and sporadic in the Balkans, they still maintain several populations of wetland species of European conservation interest, such as Campyliadelphus elodes, Drepanocladius polygamus, Hamatocaulis vernicosus, Scorpidium scorpoides, Tomentypnum nitens. The alpine grasslands are also threatened due to climate warming. The Balkan high mountain areas still preserve very diverse bryoflora. Especially areas with acidic bedrock in high elevations have special conservation interest, because they are rare and scattered in the predominantly calcareous Balkan area. The bryophyte flora of acidic soil and siliceous outcrops contains many calcifuge species regarded as rare in this region and red-listed in many SE European countries, e.g. arctic, alpine leafy liverworts such as Marsupella sphacelata, Scapania praetervisa, Solenostoma confertissimum or saxicolous species like the members of Grimmiaceae family (Grimmia caespiticia, G. reflexidens, Schistidium papillosum). In shaded limestone rocky habitats the bryophyte assemblages also contain several species of European conservation interest, e.g. Anomodon rostratus, Mannia triandra, Myurella sibirica, Taxiphyllum densifolium. On decaying wood in old forests we can also find some boreal species rare in Europe, like Buxbaumia viridis, Lophozia ascendens, L. guttulata.

Keywords: Balkan Peninsula, liverworts, mosses, rare species, habitat types
Towards a unified bryophyte names index and bryophyte checklist: a community-focused bryophyte resource

Michelle J. Price¹, John J. Atwood², Matt von Konrat³ & John C. Brinda²

¹ Conservatory and Botanical Garden of the City of Geneva, 1292 Chambésy-Geneva, Switzerland (michelle.price@ville-ge.ch); ² Missouri Botanical Garden, St. Louis, MO 63110, U.S.A.; ³ The Field Museum, Chicago, IL 60605, U.S.A.

Keywords: Bryophytes, nomenclature, name registration, global checklist

Our aim is to merge the three bryophyte names indexing initiatives, Index Muscorum, Index Hepaticarum and the Early Land Plants Today project, and use our combined resources to produce and maintain a single, centralized reference database for all bryophyte names: a unified *Bryophyte Names Index*. This single index will serve as a community-managed reference for bryophyte taxonomy, nomenclature and systematics, as well as being a focal point for bryologists to contribute new names, make corrections to existing entries, and resolve outstanding nomenclatural issues. Such a unified index will also serve as a platform to organize data regarding references (Recent Bryological Literature), typifications, and other nomenclatural acts. We anticipate that this platform will also be used to fulfill the pending requirements for the registration of new bryophyte names. Our goal is to engage the bryological community at large (via the IAPT Bryophyte Nomenclature Committee and the International Association of Bryologists) in a bottom-up community approach to the maintenance of bryophyte name data, with all its associated metadata, in this centralized resource. In an increasingly digitally connected world pooling our resources and expertise into one community-based tool will allow us to share tasks, advance together, and work towards the production of a global bryophyte consensus checklist. A unified approach will also ensure that this taxonomic backbone of accepted names, synonyms and consensus classification will become the nomenclatural reference used by global initiatives such as the World Flora Online, Catalogue of Life Plus, and the Global Biodiversity Information Facility. The flow of digital data regarding bryophytes will be greatly enhanced if our efforts succeed.
Moss species on the move in East Antarctic terrestrial communities

Sharon Robinson¹, Melinda Waterman¹,², Diana King¹, Johanna Turnbull¹, Jessica Bramley-Alves¹, Michael Ashcroft¹, Ellen Ryan-Colton¹, Jane Wasley¹,³, Quan Hua²

¹University of Wollongong, Centre for Sustainable Ecosystem Solutions, School of Biological Sciences, Wollongong, Australia (sharonr@uow.edu.au), ²Australian Nuclear Science and Technology Organisation, Lucas Heights, Australia, ³Australian Antarctic Division, Department of Environment, Kingston, Australia

Antarctica has experienced major changes in temperature, wind speed and stratospheric ozone levels over the last 50 years. Whilst West Antarctica and the peninsula showed rapid warming and associated ecosystem change, East Antarctica appeared to be little impacted by climate warming, thus biological changes were predicted to be relatively slow. Detecting the biological effects of Antarctic climate change has also been hindered by the paucity of long-term data sets, particularly for organisms that have been exposed to these changes throughout their lives. We monitored vegetation communities in the Windmill Islands, East Antarctica from 2000 to 2014 and found significant changes in moss species composition. In addition, we have shown that radiocarbon signals preserved along shoots of the dominant Antarctic moss flora can be used to determine accurate growth rates over a period of several decades, allowing us to explore the influence of environmental variables on growth. Carbon stable isotopic measurements suggest that the observed effects of climate variation on growth are mediated through changes in water availability and most likely linked to the more positive phase of the Southern Annular Mode and changing westerly wind patterns. For cold remote locations like Antarctica, where climate records are limited and of relatively short duration, this illustrates that mosses can act as microclimate proxies and have the potential to increase our knowledge of coastal Antarctic climate change.

Keywords: (Bryophyte distribution in space and time, Antarctica, stable isotopes, climate change, growth rates)
A distinctive condition of tropical montane cloud forest is the abundant presence of bryophytes and lichens on all available substrates, from the forest floor to the canopy. These cryptogams have important ecological functions, but they are threatened by climatic change. Current elevational patterns may indicate climate dependencies of these organisms, but these patterns have been described for only few tropical mountains so far. Most of those studies were focused on epiphytes and none have previously addressed substrate-specific patterns. We therefore analyzed patterns in the abundance and diversity of bryophytes in an elevational gradient on the western slope of Baru Volcano, Panama, explicitly taking into account different substrates. The bryophyte and lichen layer was collected from 600-cm² plots on six substrate types with four replications at eight elevations along a gradient from 1900 to 3300 m a.s.l. We determined the thickness, water-holding capacity, biomass, and bryophyte richness patterns of all samples. At lower elevations, substrates had a similar biomass and water-holding capacity per area, but with increasing elevation, terricolous substrates showed the strongest increase (highest values at 3100 m). With the data currently obtained (considering the diversity of only bryophytes), this increase in biomass was not accompanied by an increase in species richness at the plot level (alpha diversity). Instead, species richness decreased with elevation in all substrates and the highest richness at high elevation was found in epiphytes rather than terrestrial species. Biomass and diversity were not correlated, and variation in both variables along elevation was substrate dependent. Local species richness is highest at the lower, warmer elevations (which, importantly, are middle elevations on the scale of the whole mountain), in all substrates except soil. Warming might thus lead to higher local species richness at the higher elevations, but it would probably reduce richness at the lower elevations (1900 and below, outside the range studied here) as the warm tropical lowlands are known for holding fewer species. In any case, overall diversity would probably not increase, as there is a strong turnover of species along elevation and cold- and moisture-adapted species might be lost under warmer drier conditions.

Keywords: biomass, water-holding capacity, species richness, elevation, substrate
Morphological diversity in the peristome of the Neotropical moss Octoblepharum albidum Hedw. (Bryophyta, Octoblepharaceae)

Noris Salazar Allen

Smithsonian Tropical Research Institute. Apartado 0843-03092, Balboa, Ancón, Panama, Republic of Panama (salazarn@si.edu)

Octoblepharum Hedw. is a widely distributed tropical and subtropical moss genus. Hedwig, in his Species Muscorum Frondosorum erected the genus in 1801. The genus was described as having a simple peristome, of eight teeth, a sporangium without apophysis and male and female gametoea (flos masculus femineo) in the same plant (Hedwig, 1801). The name derives from the Greek words okto (οκτο) meaning eight and blepharis (βλεπηαρισ) (an eyelash) based on the eight-peristome teeth of the Type species O. albidum collected by Swartz in Jamaica. Today, 19 species are recognized worldwide (Salazar Allen & Chantranaorrapint 2018). Geographically, the most widely distributed species is O. albidum Hedw. It occurs in the tropics, subtropics and temperate zones. The gametophyte is characterized by loose turfs or cushions, leaves erect to patent to curved-spreading, strap-shaped apiculate and with a hyaline lamina of elongated hexagonal finely pitted leucocysts. Unlike the nearly uniform gametophyte morphology, the sporophyte, displays a wide range of variation in peristome morphology. Three main types of peristome are distinguished. The first type is represented by the peristome of the Type specimen with eight solid teeth composed of two outer rows of cells with faint wall striations and obtuse apex. Variations from this type include additional rows of cells, mainly towards base of teeth, pronounced vertical cell wall striations, foveolae, few apertures and obtuse to acute apices. The second type consists of teeth with wide basal apertures separating the two outer rows of cells, mostly acute apices and cell walls with vertical striations. The third type has smooth, paired short teeth with obtuse apices. These three types of peristomes and their variations occur throughout the Neotropics. A hypothesis on the evolution of these peristome types is presented.

Hedwig, J. 1801. Species Muscorum Frondosorum, descriptae et tabulis aeneis LXXVII coloratis illustratae, sumtu Joannis Ambrosii Barthii.

Key words: O. albidum peristome, smooth, diverse ornamentations, apertures, pairing teeth.
Presentation type: Oral Presentation, Poster Presentation

Abstract Title: Changes in the nomenclature of liverworts and hornworts 2013-2019. What has happened since the World Check List was finished?

Lars Söderström

1Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway (lars.soderstrom@ntnu.no).

In 2016 the World Check List of Horn- and Liverworts was published. It was built on an 8-year long work involving 40 co-authors and some additional contributors. The cut-off for accepting any further nomenclatural or taxonomic changes was set to 1 July 2015. Thus, the checklist is a snapshot of the knowledge that day! The ELPT project is continuously registering changes and is feeding Catalogue of Life with the latest updates once a year (including distribution but not yet synonymy). In this presentation we will outline the changes happened from the publication of the WCL until today, to give an idea of how much the taxonomic work is changing our view on the group.

Keywords: Liverworts, Hornworts, Taxonomic and Nomenclatural changes
The bryophyte flora of the Netherlands has been extensively studied and is considered well known. However, problems with morphological species delimitations still hamper the recognition of several taxa, especially in taxonomically difficult genera and species complexes. To test whether the current number of 600 species correctly represents the bryophyte diversity of the Netherlands, Naturalis and the Dutch Bryological and Lichenological Society (BLWG) carried out an integrative project combining DNA barcoding and analysis of morphological (and ecological) characters. \textit{Trn}L-F and ITS sequences were generated from almost all bryophyte taxa currently occurring in the Netherlands. Based on the comparison of genetically distinct groups with morphologically defined species and morphometric analyses in difficult taxa, we conclude that the bryophyte diversity in the Netherlands has been underestimated by at least 10\% when based on morphology alone. At least 21 species and subspecies were newly discovered for the country (including three species new to science), the previously uncertain presence of another 45 taxa was confirmed, and few previously recognized species were excluded from the Dutch bryoflora. Species delimitations in difficult genera such as \textit{Bryum}, \textit{Drepanocladus}, \textit{Fissidens}, \textit{Schistidium}, \textit{Trichostomum}, \textit{Ulota}, \textit{Warnstorfia}, and \textit{Weissia} could be clarified. Morphological characters and ecological preferences were assessed in terms of their suitability to be used for field identification and in revised identification keys. The results are expected to facilitate the identification and use of bryophytes in biodiversity assessments and environmental monitoring in Western Europe.

**Keywords:** DNA barcoding, Dutch bryoflora, integrative taxonomy, species delimitation
Disentangling the hidden diversity within the widespread moss *Lewinskya affinis* (Orthotrichaceae).

B. Vigalondo*1, R. Garilleti2, A. Vanderpoorten3, J. Patiño4, I. Draper1,5, J.A. Calleja5,6, V. Mazimpaka1,5 & F. Lara1,5.

1 Departamento de Biología (Botánica), Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, 28049, Spain (*beavigal@gmail.com); 2 Departamento de Botánica y Geología, Facultad de Farmacia, Universidad de Valencia, Burjassot, 46100, Spain; 3 Institute of Botany, University of Liège, B22 Sart Tilman, B-4000 Liège, Belgium; 4 Plant Conservation and Biogeography, Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, La Laguna, 38071, Spain; 5 Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM); 6 Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Cerdanyola del Vallès, Spain.

The high capacity for long distance dispersal and relative low diversification rates of bryophytes arise as one of the mechanistic hypotheses to explain the strikingly lower number of species, in particular of endemics, and the larger distribution ranges in comparison with angiosperms. We test here these assumptions using as a model *Lewinskya affinis* (≡ *Orthotrichum affine*), a moss species widely distributed across the western Palearctic, eastern Africa and the western Nearctic. Within an integrative taxonomy framework, we generated competing taxonomic hypotheses derived from separate and combined analyses of multilocus sequence data, morphological characters, and geographical distributions. The taxonomical hypotheses were then validated under a Bayes factor molecular delimitation approach.

Our results suggest that *Lewinskya affinis*, as currently conceived, comprises no less than seven distinct sibling species, including *L. affinis s.str.*, *L. fastigiata* and *L. leptocarpa*, three species so far considered synonyms, plus four new species. We provide morphological traits for the identification of the seven species, as well as their known distribution ranges. Noteworthy, none of the species exhibits a trans-oceanic range, which suggest, on one hand, that the broad distributions typically exhibited by moss species could largely result from taxonomic shortcomings, and, on the other hand, that there is a tendency for a within-continent diversification rather than recurrent dispersal following speciation.

Keywords: Diversification, Integrative taxonomy, Long-distance dispersal, *Orthotrichum affine*. 
Mosses as Bioindicators of Metal Contamination in Karst Bauxite, northern Guizhou, China

Dengfu Wang\textsuperscript{1,2}, Zhaohui Zhang\textsuperscript{2}

\textsuperscript{1}Institute of Karst Science, Guizhou Normal University, Guiyang 550001, Guizhou, P.R. China (wangdengfu1234@126.com); \textsuperscript{2}Key Laboratory for Information System of Mountainous Area and Protection of Ecological Environment of Guizhou Province, Guizhou Normal University, Guiyang 550001, Guizhou, P.R. China (zhaozhang9@hotmail.com)

Bauxite mining on karst provokes numerous ecological and environmental problems, including metal pollution, water and soil erosion, and the destruction of vegetation. Among them, the most important environmental problem consists in soil metal pollution. Mosses are often used as bioindicators to assess levels of metal contamination in soil.

Supported by the National Natural Science Foundation of China (NSFC No.31760050 and No.31360043), three bryological surveys were conducted in karst bauxite, northern Guizhou, China. The objective of this study was to determine whether mosses could be used as bioindicators of metal contamination in abandoned karst bauxite mine.

Mosses were collected from an abandoned karst bauxite mine at Shangdong, Xiuwen County, northern Guizhou Province, China. Three dominant mosses were collected and identified as \textit{Barbula rigidula} (BR), \textit{Semibarbula orientalis} (SO), and \textit{Barbula vinealis} (BV). The concentrations of Al, Fe, Cu, and Zn were analyzed by inductively coupled plasma mass spectrometry (ICP-MS).

Levels of four metal elements (Al, Fe, Cu, and Zn) were determined in the three moss species, where concentrations of Al, Fe, Cu, and Zn, respectively, resulted to be 2,491-95,580 mg/kg, 3,635-65,870 mg/kg, 72.7-148.2 mg/kg, and 7.4-387.1 mg/kg. The results showed that the metal content determined in mosses was relatively high, and easily exceeded the background value for Guizhou Province, particularly in the moss BR. The metal contents also differed in the three mosses: BR > SO > BV. Data also suggested that BR colonies were able to tolerate and accumulate high levels of metal elements, which evidences their suitability to be used as a bioindicator of soil metal contamination provoked by mining activities.

Keywords: Mosses, metal contamination, bioindicators, abandoned karst bauxite, Guizhou
Molecular basis of convergent evolution: parallel reduction of the sporophyte phase in mosses

Alexander Kirbis\(^1\), Manuel Waller\(^1\), Anna Neubauer\(^1\), Stefan A Rensing\(^2,4\), Nico van Gessel\(^3\), Ralf Reski\(^3,4\), Daniel Lang\(^5\), Karen Hicks\(^6\), Peter Szovenyi\(^1\)

\(^1\) Department of Systematic and Evolutionary Botany, University of Zurich, Zurich, Switzerland (alexander.kirbis@uzh.ch); \(^2\) Philipps University Marburg, Marburg, Germany; \(^3\) Plant Biotechnology, University of Freiburg, Freiburg, Germany; \(^4\) BIOSS Centre for Biological Signalling Studies, Freiburg, Germany; \(^5\) Helmholtz Zentrum München, Munich, Germany; \(^6\) Kenyon College, Ohio, Ohio, USA

The phenomenon of convergent evolution, the repeated evolution of traits in independent lineages, provides ideal replicates to test for constraints on the trajectory of evolutionary processes. We aim at investigating the molecular mechanisms of convergent evolution by studying the evolutionary-developmental mechanisms underlying the repeated evolution of reduced sporophyte phenotypes in the moss family Funariaceae.

Recent research on the phylogeny of the family has shown that a highly reduced sporophyte phenotype has evolved multiple times independently. This repeated morphological reduction, the simple structure of the sporophyte phase, and the amenability for reverse genetic work makes the Funariaceae family an ideal model system to study convergent evolution in a set of closely related taxa. We have chosen two species that represent the end-points of sporophyte complexity within the family. *Funaria hygrometrica* has an elongated seta and specialized structures for controlled spore release, while *Physcomitrella patens* exhibits a reduced sporophyte phenotype, characterized by a short seta and a simple spherical capsule.

The molecular mechanisms connected to the evolution of convergent phenotypes are diverse. To get an overview of the transcriptional landscape of sporophyte development, we extracted and sequenced RNA from four developmental stages of sporophytes from both species. The prediction of orthologous genes allowed us to directly compare expression patterns of conserved genes between the two model organisms. We identified known regulators of sporophyte development, as well as a set of genes involved in phytohormone synthesis, signalling, and other cellular processes that are differentially expressed between the two species. We could also determine that a large fraction of genes specifically expressed during sporophyte development have no orthologous relationships. Furthermore, we used co-expression network analysis to identify new regulatory connections potentially contributing to the evolution of divergent sporophyte phenotypes. Taken together, our analyses suggest that both, rewiring of existing regulatory networks and the addition of non-conserved genes to regulatory cascades, have contributed to the evolution of a reduced sporophyte phenotype in Funariaceae.

Keywords: Funariaceae, Sporophyte development, Convergent Evolution, Transcriptomics, Molecular Evolution
Testing the evolutionary history of *Ceratodon purpureus*, the sister species *C. amazonum*, and the recombinant *C. ×conicus*

Marta Nieto-Lugilde¹, Olaf Werner¹, Sarah B. Carey², Stuart F. McDaniel² & Rosa M. Ros¹

¹ Departamento de Biología Vegetal, Facultad de Biología, Universidad de Murcia, Campus de Espinardo, 30100 Murcia, Spain (manilu@um.es); ² Biology Department, University of Florida, Gainesville, Florida 32611, USA.

The difference in time scale between the evolution or reproductive isolation and changing ecological circumstances means that current species ranges are likely to be imperfect proxies for distributions at the time of speciation. Statistical analysis of current genetic structure and diversity in populations of related species can identify historical processes of vicariance, history of dispersion, and episodes of expansion and contraction of population sizes, and provide insights into the speciation process. Evaluating the demographic history of speciation requires a quantity of genetic data which has been generated for relatively few bryophyte species. We employed coalescent analyses of nucleotide polymorphism data to reconstruct the demographic and evolutionary history of the cosmopolitan moss *C. purpureus*, the recently discovered sister species *C. amazonum*, and the recombinant *C. ×conicus*. For these aims, population genetic summary statistics were calculated, demographic parameters (divergence time, effective population sizes and migration rates) were estimated and evolutionary scenarios were simulated. Moreover, we calculated if hybridization between parental taxa occurred in one or several events. We found evidence for asymmetric gene flow between *C. purpureus* and *C. amazonum*, favoring introgression from the common, cosmopolitan species into the rare southern European species. We estimated the effective population size of *C. amazonum* to be smaller than *C. purpureus*. These observations suggest that if the event that produced these two daughter species involved a population bottleneck, the effective population size of *C. amazonum* has recovered relatively quickly, potentially as a consequence of recurrent gene flow from *C. purpureus*. Finally, we find clear evidence that *C. ×conicus* was formed by multiple hybridization events between *C. purpureus* and *C. amazonum*, further supporting the role of gene flow in the speciation process in bryophytes.

Keywords: demographic history, evolutionary biology, gene flow, speciation process, southern Europe
Light and phyto-hormone interplay in development of Physcomitrella patens

Durga Prasad Biswal, Kishore CS Panigrahi

Plant Biology Lab (http://www.niser.ac.in/~panigrahi/)
School of Biological Sciences
National Institute of Science Education and Research (NISER), HBNI
Bhubaneswar, Jatni, Odisha, India, 752050

1 panigrahi@niser.ac.in

Plant growth and development is controlled by a crosstalk among different internal factors and environmental cues. Light is one of the major environmental signal regulating plant development. Phytohormones, on the other hand, modulate different internal responses of plants. How light and hormone together regulate the plant responses is a focused area of research. Majority of work in this concern has been carried out mainly in higher plants such as Arabidopsis thaliana. In Arabidopsis phytochromes and cryptochromes have been shown to inhibit response of plant hormones such as auxin. But how the light-hormone crosstalk modulates the development in lower plants like mosses is not well understood. In this study, we investigated the light and hormone interaction in moss Physcomitrella patens using different mutants. We have evaluated the response of WT, phytochrome (phy1, phy3) and fhy1 mutants of Physcomitrella under different light conditions in presence or absence of auxin and cytokinin. The plants were cultured under long day (LD) condition (16 hour light/8 hour dark) in all the light conditions used. We made the following observations:

1) Under far-red (FR) light LD cycle caulonema differentiation was promoted in WT plants. Furthermore, caulonema induction was independent of exogenous auxin under FR light.
2) Cytokinin mediated bud formation was inhibited under FR light.
3) Cytokinin mediated bud formation under red light was enhanced by glucose in Physcomitrella.
4) phy1, phy3 and fhy1 mutants displayed differential sensitivity to auxin and cytokinin in terms of chloronema-caulonema transition and bud induction.
5) Results suggested that the functions of phytochromes are redundant and FHY1 may play a major role in protonema differentiation and bud induction in Physcomitrella.

Key Words: Physcomitrella patens, Light, auxin, cytokinin, FHY1
Gene transfer across species boundaries in bryophytes: evidence from major life cycle stages in *Homalothecium lutescens* and *H. sericeum*

Weerachon Sawangproh1,4*, Lars Hedenäs3, Annick. S. Lang1, Bengt Hansson2, and Nils Cronberg1

1 Biodiversity, Department of Biology, Lund University, Ecology Building, Lund, Sweden
2 Department of Biology, Lund University, Ecology Building, Lund, Sweden
3 Department of Botany, Swedish Museum of Natural History, Stockholm, Sweden
4 Program in Conservation Biology, School of Interdisciplinary Studies, Mahidol University (Kanchanaburi Campus), 199 Moo 9, Lumsam, Sai Yok District, Kanchanaburi Province, Thailand
* Corresponding author: weerachon.sawangproh@biol.lu.se

The mosses *Homalothecium lutescens* and *H. sericeum* are genetically, morphologically and ecologically differentiated, but mixed populations sometimes occur. We determined genotypes using SNP markers to estimate the degree of genetic mixing in 449 moss samples collected from seven sympatric and five allopatric populations on Öland, south Sweden. The samples represented three generations: haploid maternal gametophytes, diploid sporophytes, and haploid sporelings. Admixture analyses identified a majority of pure *H. lutescens* and *H. sericeum* samples, but 76 samples were identified as mildly admixed (17%) and 17 samples (3.8%) as strongly admixed. Admixed samples were represented in all three generations in several populations. Hybridization and introgression were bidirectional. Our results demonstrate that admixed genomes are transferred between the generations, so that the populations behave as true hybrid zones. Earlier studies of sympatric bryophyte populations with admixed individuals have not been able to show that admixed alleles are transferred beyond the first generation. The presence of true hybrid zones has strong evolutionary implications because genetic material transferred across species boundaries can be directly exposed to selection in the long-lived haploid generation of the bryophyte life cycle, and contribute to local adaptation, longtime survival and speciation.

Keywords: Admixture, Recombinants, STRUCTURE, PCoA, Hybrid Index
Abstract Title: Population genomics of a Southern Appalachian bryophyte with extreme sex allopatry

1 J.C. Villarreal, Marta Alonso García, Kenneth McFarland, Bernard Goffient

Affiliations: 1, Integrative and System Biology Institute, Department of Biology, Laval University, Quebec, Canada; 2University of Tennessee, Department of Botany, 437 Hesler Biology Bldg, 1406 Circle Drive, Knoxville, Tennessee, 37996-1100, USA; 3University of Connecticut, Ecology and Evolutionary Biology, 75 North Eagleville road, Storrs, CT, 06269-3043, USA

The southern Appalachian Mountains (SAM) is one of the most biodiversity-rich areas within North America and has been considered a refugium for many disjunct plant species. Extreme examples of disjunct bryophyte taxa include the liverwort Acrobolbus ciliatus, known only as males in Japan and females in the SAM. Extreme sex allopatry may have profound implications on the genetic diversity of the species and potentially leading to local extinction. Our study focuses on a SAM hornwort, Nothoceros aenigmaticus (R. M. Schust.) J. C. Villarreal & K. D. McFarland. This hornwort was described from North Carolina and it's widespread in the SAM, growing on rocks near streams in six watersheds of the Tennessee River. The species reproduces clonally; males and females occur in different watersheds, ca. 30 miles apart. Nothoceros aenigmaticus has been recently found in Mexico, where it reproduces sexually. Here we test whether there is a genomic imprint from such extreme case of sex allopatry or whether the genomic diversity is partitioned by watersheds.

We have answered these questions using nuclear and organellar microsatellites from 250 individuals from six watersheds (7 populations) in the SAM and two populations from Mexico (23 individuals). We, then, selected 86 individuals from seven populations and used genotyping by sequencing to obtain over 600 bi-allelic markers. The phylogenetic analysis forms four clusters: Mexico (as the outgroup), male plants (Little Pigeon and Pigeon river watersheds) and two cluster of female plants: 1) Little Tennessee and Hiwassee River and 2) Ocoee and Coosa River. All cluster have high population differentiation (Fst values of 0.9). In addition, our individual assignment analyses and PCAs corresponded to the phylogenetic results grouping the SAM samples in three clades and recovered that males and female plants have high population differentiation (Fst values over 0.6 using microsatellites and biallelic markers).

Our results point to an extreme sex biased ratio confirmed by genomic data and, at least three potential dispersal events into the SAM in the Pleistocene. SAM Nothoceros aenigmaticus seems to be in a dead-end situation only surviving through clonal reproduction.

Keywords: Hornworts, Southern Appalachians, sex allopatry, phylogeography, asexual reproduction
Comparative genomic analysis and genetic variation within the leafy liverwort genus Scapania

Adam Vivian-Smith¹, David Long², Maren Flagmeier³, Jørund Rolstad¹ and Kristian Hassel⁴

¹ Department of Forest Genetics and Biodiversity, Norwegian Institute of Bioeconomy Research, Høgskolevein 8, 1432, Ås, Norway, (adam.vivian-smith@nibio.no); ² Royal Botanic Gardens Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, UK; ³ Department of Biology (Botany), Faculty of Sciences, Universidad Autónoma de Madrid, C/ Darwin 2, 28049 Madrid, Spain; ⁴ Department of Natural History, NTNU Univ. Museum, Norwegian Univ. of Science and Technology, NO-7491 Trondheim, Norway (kristian.hassel@ntnu.no)

The genus Scapania comprises a group of leafy liverworts distributed throughout many bryophytic assemblages. While many Scapania species grow widely, some are assessed as endangered and appear to be specialists with distinct niche environments. Several are found only in alpine forest communities, inhabiting decaying logs in streams, typical of an environment that is threatened by both logging activity and changes to watercourses. Another species, S. nimbosa, has an unusual Oceanic-Montane distribution across Ireland, Scotland, Norway, China and Nepal. Since gemmae and sexual reproduction are absent the species is hypothesized to be primarily dispersed by fragmentation. In Norway S. nimbosa occupies an area of only 13 x 20 km, at altitudes between 300-980 m, and is frequently found with another more abundant asexual species, S. ornithopodioides. This makes S. nimbosa susceptible to local extinction through climate change or perhaps interspecific competition. Genomics is being increasingly used to infer demography and the evolutionary history of a species. Ascertaining levels of genetic variation can also contribute towards an effective conservation management plan. Besides, very little is known about the genomic organization and sexual determination in leafy liverworts. To generate new knowledge about the genus Scapania we sequenced the genomes of the sexual species S. nemorea (both male and female isolates), S. undulata (a single isolate), and several asexual S. ornithopodioides and S. nimbosa isolates. Illumina paired-end (2x 300 bp) and Oxford Nanopore long reads were used to create genomic references. Initially organellar genomes were assembled, annotated and genetic variation was discovered. This revealed that variation is indeed present even for S. nimbosa and S. ornithopodioides at Norwegian sites. Next we focussed on creating a high quality nuclear reference genome for S. nemorea using the SPAdes assembler (v3.13). Qualities of each assembly and isolate were assessed with QUAST and BUSCO. While one assembly spans 202.6 Mb (10930 scaffolds; N50 of 66 Kb), other isolates of S. nemorea show larger assembled genome sizes and different Kmer distributions, consistent with the expected alternative sexual chromosome complement. We further analyse genomic synteny and diversity, but emphasize that difficulties in extracting DNA from herbarium specimens really hamper analysis.

Keywords: Scapania, genomic analysis, genetic variation, colonization, sex chromosomes
Contemporary understanding of epigenetics encompasses the study of changes in gene function that are heritable and do not entail a change in DNA sequence. Although these changes comprise histone variants, posttranslational modifications of amino acids on the amino-terminal tail of histones, and covalent modifications of DNA bases, most research on epigenetics focuses on DNA methylation. One elegant way to study differences in DNA methylation between samples is based on bisulfite sequencing. This technique takes advantage of the fact that sodium bisulfite causes the deamination of cytosines, unless they are protected by methylation. This results in a uracil residue, which is later converted into thymine by a PCR reaction using a compatible polymerase. With the introduction of Next Generation Sequencing (NGS) platforms, scientists became aware of the possibility of obtaining the methylation pattern of all cytosines of a given genome. While whole genome bisulfite sequencing has many advantages when studying model organisms with a known genome sequence, it cannot be applied to non-model organisms, because of the absence of a reference genome. Reference-free reduced representation bisulfite sequencing makes it possible to study the DNA methylation of thousands of markers of a high number of individuals in natural populations of non-model organisms with NGS techniques.

In this work, we present a modification of the epi genotyping by sequencing (epi-GBS) protocol that requires the use of only one hemimethylated common adapter, which is combined with unmethylated barcoded adapters. Unlike other comparable methods like epi-GBS and BsRADseq, which require the use of a higher number of methylated DNA oligos with a significant cost, in our protocol, the unmethylated cytosines of one chain of the barcoded adapter are replaced by methylated cytosines using nick translation with methylated cytosines in dNTP solution. The basic version of our technique uses only one restriction enzyme, and as a result, genomic fragments are integrated into two orientations with respect to the adapter sequences. Comparing the sequences of two chain orientations makes it possible to reconstruct the original sequence before bisulfite treatment with the help of standard software and newly developed software written in C.

Keywords: epi genotyping by sequencing, epigenetics, population genetics, reduced representation bisulfite sequencing
The contribution of gene flow to speciation is controversial since it has been reported as both a constraining and a promoting factor depending on the groups of organisms investigated. Recent studies indicate that gene flow is a potentially important factor for speciation in plants. Peatmosses (*Sphagnum* spp.) are a species-rich plant genus with high ecological and morphological plasticity, especially in the Northern Hemisphere. Peatmosses are a phylogenetically old group, but most extant species originated through a recent radiation, and hybridization among taxa is common. Most peatmosses are haploid and have small genome sizes, which makes them an excellent model for studying speciation-with-gene-flow on the genomic level. In this study, we use whole-genome resequencing to quantify genetic distance within and between several peatmosses as a proxy for gene flow and to explore phylogenetic relationships between species. We produced low depth (2-12×) whole-genome shotgun resequencing data for 99 individuals from 12 haploid peatmoss species sampled in several localities in Norway and Austria. A draft genome of *Sphagnum magellanicum* was used as a mapping reference. Overall, Nei’s mean genetic distance based on 22000 unlinked SNPs was low (0.029±0.037, mean±SD) within species and high (0.33±0.07) between species. This observation was further supported by phylogenetic analysis using nuclear and plastid genomes resolving almost all species as well-supported monophyletic clade. Phylogenies based on nuclear and plastid genomes were congruent with each other and with previously published phylogeny of the genus. One of the species, *S. lindbergii*, was placed within subgenus *Cuspidata* and as a sister clade to subgenus *Acutifolia* in phylogenies based on nuclear and plastid genomes, respectively. This indicates potential homoploid hybrid origin of this species. All species were phylogenetically highly distinct, but no clear geographical structure was observed within species. Together with the genetic distance estimates, this pattern might indicate that level of intraspecific gene flow in haploid peatmoss species is high, whereas interspecific gene flow is detected, but more restricted. Work in progress aims to quantify the levels of gene flow and to explore how differences in gene flow are associated with life-history traits, relatedness and populations genetic parameters of the studied species.

Keywords: peatmoss, hybridization, gene flow, population genomics, speciation.
The gene regulatory map of *Physcomitrella patens* life cycle reveals key components of the developmental transitions modulated by membrane-anchored calpain DEFECTIVE KERNEL 1

Viktor Demko¹, Tatiana Belova², Pierre-François Perroud³, Thorgeir R. Hvidsten², Wenche Johansen⁴, Boris Bokor¹, Maxim Messerer⁵, Klaus Mayer⁵, Odd-Arne Olsen⁷, Daniel Lang⁵

¹Department of Plant Physiology, Faculty of Natural Sciences, Ilkovicova 6, 84215 Bratislava, Slovakia (viktor.demko@uniba.sk), ²Norwegian University of Life Sciences, POBox 5003, NO-1432 Aas, Norway, ³Faculty of Biology, Philipps University of Marburg, Karl-von-Frisch- Straße 8, D-35043 Marburg, Germany, ⁴Inland Norway University of Applied Sciences, Holsetgata 22 N-2317 Hamar, Norway, ⁵Plant Genome and Systems Biology, Helmholtz Zentrum München, Ingolstädter Landstraße 1, D-85764 Neuherberg, Germany

Recent work in land plants supports an intriguing evolutionary phenomenon where conserved developmental regulators are co-opted to control diverse morphogenetic programs. The membrane-anchored calpain DEFECTIVE KERNEL 1 (DEK1) has been implicated in positional signalling required for cell fate control during embryogenesis, shoot meristem formation and endosperm development in seed plants. In the moss *P. patens*, DEK1 is essential for oriented cell divisions that lead to the transition from filamentous growth to organized three-dimensional growth, but also effects other phases of the life cycle. During its life cycle, *P. patens* undergoes additional developmental switches that lead to the formation of new cell types and major body plan reorganizations. So far, only few associated regulators have been identified. In order to elucidate the complex effect of DEK1 on the *P. patens* transcriptome, we first constructed a global regulatory network (GRN) using Gene Network Inference with Ensemble of trees (GENIE3) based on 299 *P. patens* atlas transcriptome libraries representing most *P. patens* tissues, seventy four libraries from five different DEK1 genotypes (WT, dek1 deletion mutant, mutants carrying internal DEK1 domain deletions and DEK1 over-expressing line) harvested at five times points and a set of 1700 regulators. Partitioning of the generated GRN resolved eleven subnetworks representing distinct phases of the *P. patens* life cycle. Here, we describe the effect of DEK1 on transcripts involved in *P. patens* gametophyte development, including the chloronema-to-caulonema transition, bud initiation and gametophore development together with recent genetic analysis that provide additional clues to the DEK1 function in plant morphogenesis. This project is supported by the Slovak Research and Development Agency grant APVV-17-0570.

**Keywords:** (no more than 5 words or short phrases, to help organizing the program)
Cell fate control, Gene regulatory networks, Developmental transitions, Plant calpain
Chromosomal-scale assembly of the *M. polymorpha* genome reveals similarities and differences to *P. patens* and *A. thaliana* genomes with respect to DNA-methylation and recombination rate

Seydina Issa Diop¹, Alexander Kirbis¹, Anna Neubauer¹, Danny Duijsings⁴, Walter Pirovano⁴, Elena Conti¹, Ueli Grossniklaus², Hanna Kokko³, Péter Szövényi¹

1. Department of Systematic and Evolutionary Botany & Zurich-Basel Plant Science Center, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland
2. Department of Plant and Microbial Biology & Zurich-Basel Plant Science Center, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland
3. Department of Evolutionary Biology and Environmental Studies, University of Zurich Winterthurerstrasse 190 8057 Zurich
4. BaseClear B.V., Sylviusweg 74,2333 BE, LEIDEN, The Netherlands

Author for correspondence: Peter Szövényi, peter.szoevenyi@uzh.ch, Dept. of Systematic and Evolutionary Botany, University of Zurich, Zollikerstr 107, 8008 Zurich, Switzerland. Phone: +41 (0) 634 84 40

*Marchantia polymorpha* has recently become a prime model for cellular, evo-devo, synthetic biological, and evolutionary investigations. We present a chromosomal-scale assembly of the *M. polymorpha* genome making comparative genome structure analysis and classical genetic mapping approaches feasible.

We anchored 88% of the *M. polymorpha* draft genome to a high-density linkage map resulting in eight pseudomolecules. We found that the overall genome structure of *M. polymorpha* is in some respects different from that of the model moss *Physcomitrella patens*. Specifically, recombination rates are greatest in the middle of the chromosome arms like in most vascular plant genomes, which is in contrast to *P. patens* where recombination rates are evenly distributed along the chromosomes. Nevertheless, some other properties of the genome are shared with *P. patens*. As in *P. patens*, DNA methylation in *M. polymorpha* is spread evenly along the chromosomes, which is in stark contrast to *Arabidopsis thaliana*, where DNA methylation is strongly enriched at the centromeres. Nevertheless, DNA methylation and recombination rate are anticorrelated in all three species.

Taken together, the chromosomal-scale genome assembly we present opens new avenues for *M. polymorpha* research by linking the physical and genetic maps, making novel genomic and genetic analyses, including map-based cloning, feasible.

Key words: DNA methylation, chromosome-scale assembly, evolution, large-scale genome structure, bryophytes, recombination rate
PEATmoss (Physcomitrella Expression Atlas Tool): a unified gene expression atlas and gene model lookup database for *Physcomitrella patens*

Noe Fernandez-Pozo¹, Fabian B. Haas¹, Rabea Meyberg¹, Kristian K. Ullrich¹,², Manuel Hiss¹, Pierre-François Perroud¹, Sebastian Hanke¹, Viktor Kratz¹, Adrian Powell³, Eleanor F. Vesty¹, Chris Daum⁵, Matt Zane⁵, Anna Lipzen⁵, Avinash Sreedasyam⁶, Jane Grimwood⁶, Juliet C. Coates⁴, Kerrie Barry⁵, Jeremy Schmutz⁶, Lukas A. Mueller³, Stefan A. Rensing¹,²

¹Plant Cell Biology, Faculty of Biology, University of Marburg, Marburg, Germany (noefp@uni-marburg.de, stefan.rensing@biologie.uni-marburg.de); ²Department of Evolutionary Genetics, Max Planck Institute for Evolutionary Biology, Ploen, Germany; ³Boyce Thompson Institute, Ithaca, NY, USA; ⁴School of Biosciences, University of Birmingham, Birmingham, UK; ⁵US Department of Energy (DOE) Joint Genome Institute, Walnut Creek, CA, 94598 USA; ⁶HudsonAlpha Institute for Biotechnology, Huntsville, AL, 35806 USA; ⁷BIOSS Centre for Biological Signalling Studies, University of Freiburg, Freiburg, Germany.

*Physcomitrella patens* resources are of great importance for comparative genomics and evo-devo approaches. However, publicly available expression data from *P. patens* were so far produced in three different technologies, Combimatrix and Nimblegen expression microarrays and RNA-seq, using gene annotation versions 1.2, 1.6 and 3.3, respectively. Three tools host some of these data, Genevestigator, the *P. patens* eFP Browser and Phytozome. However, these tools are limited to data from one single gene version or technology, few data sets and few visualization methods. Genevestigator, in the non-commercial version, is limited to few visualization plots for one single query gene from v1.2. The eFP Browser is limited to query one single gene in only one data set from gene v1.6. Phytozome contains RNA-seq expression data for the current gene annotation v3.3, but the only visualization method is an HTML table with gene expression values for only one gene.

Here, we present PEATmoss (https://peatmoss.online.uni-marburg.de), a new expression atlas for *P. patens* integrating gene expression data from all the mentioned platforms and tools. It contains 109 experiments classified in 9 data sets, of which 35 are new experiments not available in any other tool. PEATmoss is very interactive and provides visualization methods such as a 3D expression cube, expression data in cartoons, bar plots, hierarchical clustering heatmap, scatterplot and tabular data downloading. The expression cube shows gene expression for the query gene and co-expressed genes, a custom list of genes or the output from BLAST, allowing multiple gene comparison. Additionally, a lookup database was developed and integrated to automatically convert between gene versions to facilitate querying expression data from any gene and data set. Furthermore, the lookup database contains tools for bulk gene conversion and sequence downloading, and provides cross link annotations for *P. patens* genes to NCBI, Phytozome, Ensembl Plants, TAIR, PLAZA, CoGe, TAPscan and genome browsers.

**Keywords:** Bioinformatics, gene expression, gene annotation, webtool, *Physcomitrella patens*, comparative genomics
Evolutionarily distinct pathways are present to regulate chloroplast proliferation in the moss, *Physcomitrella patens*

Tomomichi Fujita¹, Prapaporn Pongthai², Huong Thi Do², Natsumi Inoue², Yasushi Yoshioka³, Hiroyoshi Takano⁴

¹Faculty of Science, Hokkaido University, Sapporo, 060-0810, Japan (tfujita@sci.hokudai.ac.jp); ²Graduate School of Life Science, Hokkaido University, Sapporo, Japan; ³Graduate School of Science, Nagoya University, Nagoya, Japan; ⁴Graduate School of Science and Technology, Kumamoto University, Kumamoto, Japan

Recent studies reveal that many bacteria have distinct pathways to divide in accordance with surrounding conditions. Although mitochondria and chloroplasts as endosymbiotic organelles, which are originated from alpha proteolytic bacteria and photosynthetic cyanobacteria, respectively, have to divide as host cell divides, it is still largely unknown whether organelle proliferation is subject to such distinct regulation under different developmental contexts or environmental conditions within the host cells. Here we studied proliferation of chloroplasts under different environmental conditions in the moss, *Physcomitrella patens*. In the moss, under a general culture condition, chloroplasts proliferation is dependent of peptidoglycan (PG), which is well conserved and essential for bacterial cell division and considered as an anciently derived component for chloroplast proliferation in bryophytes. On the other hand, we found that, under salinity stress conditions, the proliferation of the moss chloroplasts is controlled by PG-independent pathway, which appears more similar pathway found in chloroplast division of vascular plants. Abscisic acid (ABA) emerged as an important phytohormone to salinity stress during land plant evolution and we found that ABA signalling components such as SnRK2 and ABI3, play essential roles to regulate the PG-independent chloroplast proliferation in *P. patens*. Even under non-stressed conditions, sub-population of chloroplasts fails to proliferate, becoming giant chloroplasts. This giant chloroplasts are physically separated by centrifugally expanding septum. Thus, our results provide evidence that chloroplast proliferation is regulated by PG-dependent, PG-independent pathways and physical force, which appears more divergent than we acknowledged and provides a plausible explanation why nearly all plant cells have been robustly able to maintain chloroplasts without losing after endosymbiosis establishment.

Keywords: moss, *Physcomitrella patens*, chloroplast proliferation, peptidoglycan, abscisic acid
**Presentation type:** Oral Presentation, Poster Presentation

**Investigating Myosin XI Function in *Physcomitrella patens* Tip Growth by Conditional Mutagenesis**

Giulia Galotto¹, Jeffrey Bibeau¹, Yen-Chun Liu¹, Pattipong Wisanpitayakorn², Sayed Iman Mousavi², Erkan Tüzel² and Luis Vidali¹

¹ Department of Biology and Biotechnology, Worcester Polytechnic Institute, Worcester, Ma 01601, U.S.A (ggalotto@wpi.edu)  ² Department of Physics, Worcester Polytechnic Institute, Worcester, Ma 01609, U.S.A

*Physcomitrella patens* is an ideal model system to study tip growth, which depends on the actin cytoskeleton and cell wall secretion. Myosin XI plays an essential role in tip growth: plants where myosin XI genes have been silenced exhibit an altered morphology composed of round cells. To further characterize the role of myosin XI in tip growth, we developed mutant plants in which myosin XI protein is temperature sensitive (TS) at 32°C. At 32°C, cells undergo morphological changes within 3 hr: the zone behind the tip swells, and the tip narrows. The swelling morphology of the TS plants at 32°C is different from the swelling induced by latrunculin B-treatment. The morphology differences were quantified by measuring the curvature of the tip, showing a significant change between conditions. These values are being used as input to constrain a mathematical model of tip growth. In addition, in TS plants exposed to 32°C for 24 hr, a significant number of caulonema cells die, compared to the TS at 20°C or the WT at 32°C. Surprisingly, we found that F-actin depolymerization reduces the number of dying cells. These results suggest myosin XI directs exocytosis to the cell apex determining the polarized morphology of the cell, and it is important for caulonema survival. Furthermore, in cells deprived of functional myosin XI for 1 hr, the vacuole morphology appears altered-- vacuole tubules fuse together, suggesting myosin XI is involved in vacuole homeostasis. We also used the myosin XI TS line to study the interplay between myosin XI and F-actin. Following treatment of cells with low concentration of latrunculin B, myosin XI and vesicles generate F-actin, producing motile clusters that resemble actin comet tail based motility. We used the formation of these clusters to study if myosin XI is essential for their formation. Experiments with the myosin XI TS cells expressing the vesicle marker VAMP72 and the F-actin marker lifeact-mEGFP show that the clusters do not form in myosin XI TS at the restrictive temperature. Our results suggest myosin XI is essential for cell polarization and survival, vacuole homeostasis and for the formation of F-actin-vesicles clusters.

Keywords: tip growth, myosin XI, actin cytoskeleton, membrane trafficking
Strigolactones signalling repression in land plants: Is SMXL function conserved between vascular plants and the moss *Physcomitrella patens*?

Guillory Ambre¹, Lopez-Obando Mauricio ², de Saint Germain Alexandre³, Boyer François-Didier¹,³, Rameau Catherine¹, Bonhomme Sandrine¹.

¹ Institut Jean-Pierre Bourgin – INRA Centre de Versailles-Grignon, Route de Saint-Cyr, 78026 Versailles Cedex France (ambre.guillory@inra.fr), ² Swedish University of Agricultural Sciences - BioCentre, Department of Molecular Sciences, SLU, Almas allé 5, Uppsala, Sweden, ³ Institut de Chime des Substances Naturelles - CNRS - UPR 2301, bâtiment 27, 1 avenue de la Terrasse, 91198 Gif-sur-Yvette Cedex France

Keywords: CRISPR mutagenesis, strigolactones, *Physcomitrella patens*, signalling repression, evolution, SCF complex, Clp-ATPases.

Strigolactones (SL) are the newest discovered plant hormones, which play major roles in several developmental processes in vascular plants. Notably, they repress the outgrowth of axillary buds, acting as a component of the well-known apical dominance machinery, together with auxins and cytokinines. Recent phylogenetic studies suggest that while the SL biosynthesis pathway seems to be broadly conserved across land plants, the signalling pathway as it has been partly uncovered in vascular plants appears to be a much more recent innovation. The molecular function of the SL signalling pathway’s repressors, the SMXL proteins, remains especially mysterious even in vascular plants. In the lab, we are investigating the evolution of SL signalling using three diverse plant species: *Pisum sativum*, *Arabidopsis thaliana* and the moss *Physcomitrella patens*. To uncover whether the function of SMXLs as repressors of SL signalling has been conserved across land plants’ evolution, we have devised genetical and biochemical approaches to study the four SMXL homologs of the moss *Physcomitrella patens (P. patens)*. Several combinations of *Ppsmxl* loss-of-function mutations have been obtained via CRISPR-Cas9 mediated mutagenesis to investigate the role of these genes in *P. patens’* development and sensitivity to SL. Previous characterization of the SL biosynthesis mutant *Ppccd8* has shown that SL repress filaments’ expansion in moss, making it an easy phenotype to test SL response. Characterization of a first generation of *Ppsmxl* mutants has suggested that the four genes were split between two functional clades, with only one involved in SL signalling. Additional genetic analyses using the *Ppsmxl* mutations will be carried on, such as complementation studies in the *Ppccd8* SL biosynthesis mutant. Moreover, generation of transgenic lines expressing either transcriptional or translational fusions of *PpSMXL* sequences enables us to determine where and when the PpSMXLs are expressed and whether their localization/stability is affected by SL. Biochemistry experiments such as Y2H, biFC and GFP-trapping have also been initiated in order to uncover the protein interaction network of PpSMXLs to further corroborate results from the mutants.
Single nucleotide polymorphism charting of *Physcomitrella patens* accessions

Fabian B. Haas1, Noe Fernandez-Pozo1, Rabea Meyberg1, Pierre-François Perroud1, Stefan A. Rensing1

1 Plant Cell Biology, Faculty of Biology, University of Marburg, Germany (fabian.haas@biologie.uni-marburg.de)

*Physcomitrella patens* was collected by H.L.K. Whitehouse in Gransden Wood (Huntingdonshire, UK) 1962 (Ashton and Cove 1977) and distributed across the globe starting 1974. Hence, it has been distributed in laboratories for half a decade. Today, more than 13 different pedigrees derived from Gransden are known. Additionally, accessions from other sites were collected during the last decades.

In this study we present single nucleotide polymorphism (SNP) analyses based on RNA-seq data of four different accessions (probably ecotypes) and 13 different Gransden pedigrees. SNPs were overlaid with meta data and known phenotypic variations. Defining SNPs were identified that can be used to determine the different accessions. Interestingly, independent mutations apparently came to be in the different Gransden pedigrees.


Keywords: *Physcomitrella patens*, SNP, Gransden pedigree, Ecotypes, Bioinformatics
A cis-acting bidirectional transcription switch regulates sexual dimorphism in Marchantia

Tetsuya Hisanaga1,2, Keitaro Okahashi3, Shohei Yamaoka3, Tomoaki Kajiwara3, Ryuichi Nishihama3, Masaki Shimamura4, Katsuyuki T. Yamato5, John L. Bowman6, Frederic Berger1, Takayuki Kohchi3, Keiji Nakajima2

1 Gregor Mendel Institute (GMI), Austrian Academy of Sciences, Vienna BioCenter (VBC), Dr. Bohr Gasse 3, 1030 Vienna, Austria. (Tetsuya.hisanaga@gmi.oeaw.ac.at); 2 Graduate School of Science and Technology, Nara Institute of Science and Technology, 8916-5 Takayama, Ikoma, Nara, 630-0192, Japan; 3 Graduate School of Biostudies, Sakyo-ku, Kyoto University, Kyoto 606-8501, Japan; 4 Graduate School of Science, Hiroshima University, Kagamiyama, 1-3-1, Higashi-hiroshima 739-8526, Japan; 5 Faculty of Biology-Oriented Science and Technology, Kindai University, 930 Nishimitani, Kinokawa, Wakayama 649-6493, Japan; 6 School of Biological Sciences, Monash University, Melbourne VIC 3800, Australia

Plant life cycles alternate between haploid gametophytes and diploid sporophytes. Regulatory factors determining male and female sexual morphologies have been identified for sporophytic reproductive organs, such as stamens and pistils of flowering plants. In contrast, those regulating sex-specific traits in the haploid gametophytes that produce male and female gametes and hence are central to plant sexual reproduction are poorly understood. To reveal mechanisms of sexual differentiation in gametophyte, we used Marchantia polymorpha (Marchantia), a dioicous liverwort, as a model. We focused on a gene encoding MYB type transcription factor named FEMALE GAMETOPHYTE MYB (MpFGMYB). Using expression analyses, molecular genetics and microscopic observation, we revealed function of MpFGMYB in sexual differentiation of Marchantia. Our expression analyses indicated specific expression of MpFGMYB in developing archegoniophores. Surprisingly, genetic females of Mpfgmyb developed antheridiophores instead of archegoniophores. These mutants even differentiated sperm. These sex conversion phenotypes were rescued by a transgenic copy of MpFGMYB, confirming a causal relationship between these phenotypes and MpFGMYB function. Altogether, our result clearly indicated that MpFGMYB is required for female sexual differentiation in Marchantia. Since MpFGMYB is an autosomal gene, its expression must be suppressed in males. We found that this suppression is achieved by antisense long non-coding RNA of MpFGMYB, named SUPPRESSOR OF FEMINIZATION (SUF). Genetic males of suf mutants exhibited male-to-female sex conversion phenotype accompanied by ectopic expression of MpFGMYB. Additional Mpfgmyb mutation suppressed this phenotype. Altogether these results clearly demonstrated that bidirectional transcription of MpFGMYB acts as a toggle between female and male sexual differentiation in Marchantia gametophytes. Arabidopsis thaliana MpFGMYB orthologues are known to promote development of embryo sacs, highly reduced female gametophytes. Thus, members of FGMYB subfamily transcription factors regulate female gametophyte development across land plants.

Keywords: Antisense transcription, lncRNA, Marchantia polymorpha, R2R3 MYB type transcription factor, Sexual differentiation
Evolution of MurE functions from moss plastid division to angiosperm chloroplast development

Ichiro Kajisa¹, Xiaofei Lin², Yilan E², Hiromi Kudo¹, Susumu Takio³,⁴, Katsuaki Takechi³, Hiroyoshi Takano³,⁵

¹ Graduate School of Science and Technology, Kumamoto Univ., ² College of Life Sciences, Inner Mongolia Univ. ³ Faculty of Advanced Science and Technology, Kumamoto Univ. ⁴ Center for Water Cycle, Marine Environment and Disaster Management, Kumamoto Univ. ⁵ Institute of Pulsed Power Science, Kumamoto Univ.

Bacterial peptidoglycan (PG) is a continuous covalent macromolecule comprised of a sugar-amino acid polymer. We have documented that the moss Physcomitrella patens contains a set of genes capable of generating PG (Mur genes) and that knocking out these genes causes defects in chloroplast division. Recently, we were able to visualize PG in moss under epifluorescence microscopy with a novel metabolic cell wall-labeling method of d-amino acid using click chemistry (Hirano et al. 2016). Most Mur genes have been lost from the genomes of chlorophyte algae and angiosperms, suggesting that no plastid PG systems work in these species. By contrast, MurE genes, encoding an enzyme that catalyzes the formation of UDP-N-acetylmuramic acid (UDP-MurNAc) tripeptide in PG biosynthesis, are generally found in green plants, including green algae and seed plants. In contrast to the huge chloroplast phenotype in the MurE knockout lines of P. patens (Machida et al. 2006), T-DNA- tagged lines of AtMurE (atmurE mutants) displayed a white-seedling phenotype, suggesting the AtMurE is related to chloroplast development in A. thaliana (Garcia et al. 2008). Moreover, AtMurE could not rescue the macrochloroplast phenotype caused by PpMurE mutation in P. patens, showing that AtMurE is functionally divergent from the bacterial and moss MurE proteins (Garcia et al. 2008). In the sequenced gymnosperm genomes, we could identify 10 homologs of bacterial Mur genes, including MurE, suggesting the retention of the plastid PG system in gymnosperms (Lin et al. 2017). Cross-species complementation assay with MurE mutants of A. thaliana and P. patens showed that the expression of MurE cDNA from the larch, Larix gmelinii completely rescued the albepactia defects in A. thaliana but did not rescue the macrochloroplast phenotype in P. patens (Lin et al. 2017). Recently, we found that one gymnosperm MurE gene could complement both phenotypes of P. patens and A. thaliana MurE knockout plants. This may connect the functions between PG biosynthesis in moss and chloroplast development in angiosperms.

Keywords: chloroplast division, plastid gene expression, peptidoglycan, MurE,
Network of Epigenetic Regulators in Physcomitrella patens

Kapoor Meenu, Parihar Vimala, Tyagi Vidhi, Walia Akanksha and Arya Deepshikha

University School of Biotechnology, Guru Gobind Singh Indraprastha University, Sector 16C Dwarka, New Delhi-110078 India. Email: meenukapoor@me.com; meenukapoor@ipu.ac.in

Epigenetic mechanisms are regulatory processes in which DNA/histone modifications such as methylation, acetylation or phosphorylation including nucleosome repositioning lead to heritable changes in gene expression without altering the underlying nucleotide sequences in the genome. These mechanisms play crucial roles in priming plants to tolerate recurring and chronic biotic and abiotic stresses. However, there are many lacunae in our understanding of these mechanisms in stress management in flowering plants. We choose the early land plant Physcomitrella patens to understand the evolution of network of epigenetic regulators and to gain insight into how these regulators are wired and connected because around 500 million years ago in an attempt to colonize land and complete their life cycles on harsh terrestrial habitats these plants developed elaborate stress signaling pathways and robust stress tolerance machineries. Hence, using gene knockout strategies and different protein-protein interaction techniques we deciphered a well-connected network linking chromatin remodeling proteins such as the SWI/SNF-related ATP-dependent DNA helicases, chromatin modifying proteins such as the cytosine DNA methyltransferases and the polycomb repressive complex proteins that together function to maintain DNA methylation and genome integrity in P. patens genome. Based on our results we propose that activities of epigenetic regulatory proteins remained functionally relevant in early land plants where they possibly contributed in fine tuning developmental programs and in regulating physiological processes, including stress management, that eventually contributed in sustaining existence of these plants on terrestrial habitats.

Keywords: Epigenetic, DNA methylation, DDM1, Polycomb, Moss
A knockout of PpMED18 enhances salt tolerance in the moss Physcomitrella patens

Chandra Shekar Kenchappa, Mikael Ulfstedt, Guo-Zhen Hu and Hans Ronne

Department of Forest Mycology and Plant Pathology, Uppsala BioCenter, Swedish University of Agricultural Sciences, SE–750 07 Uppsala, Sweden (chandra.shekar.kenchappa@slu.se)

During stress conditions all organisms are capable of adapting to the environment by modifying gene expression through signaling pathways. The RNA polymerase II Mediator complex consists of 25–30 subunits which are evolutionarily conserved across the kingdoms and plays a vital role as a switchboard that integrates signals from different pathways to regulate gene expression. The Mediator complex consists of the Head, Middle, Tail and Cdk modules (1). We are studying the role of Mediator during abiotic stresses. We are working with the model organism Physcomitrella patens, which separated from flowering plants around 450 million years ago. PpMED18 is a single copy gene encoding a non-essential subunit in the Mediator head module. In flowering plants, MED18 is important for organ development (2). To study the role of MED18 in moss, we generated independent med18 knockout lines by using the CRISPR/CAS9 genome editing method. We found that the med18 knockout lines are phenotypically smaller in size and show a somewhat higher tolerance to salt stress than the wild type. These observations are consistent with a model where Mediator integrates the responses to different signaling pathways and balances these responses against other physiological needs such as growth (3).

Key words: Bryophyte, Physcomitrella patens, Mediator complex, Abiotic stress.

References:
The monthly transcriptome dynamics of Antarctic moss, *Sanionia uncinata* (Hedw.) Loeske, throughout the year in natural environments, reveals seasonal adaptation of extremophile plants

Jungeun Lee\(^1,2\), Hyoungseok Lee\(^1,2\), Dockyu Kim\(^3\)

\(^1\) Unit of Polar Genomics, Korea Polar Research Institute, Incheon, 21990, South Korea (jelee@kopri.re.kr); \(^2\) Polar Science, University of Science & Technology, Incheon 21990, South Korea, \(^3\)Division of Polar Life Sciences, Korea Polar Research Institute, Incheon, 21990, South Korea

Most organisms on Earth have evolved and adapted to the seasonally changing environment. The maritime Antarctic is covered with snow and ice for most of the year, but during the austral summer season, snow melts and a variety of vegetation is revealed. During this three-month period, terrestrial plants actively perform cellular activities under the prolonged daytimes. But even this short summer, the sub-zero temperatures, dryness, continuous strong light and UV radiation are very extreme conditions for plant growth, and after these summers are over, the snow starts to pile up and the plants stop growing and enter dormancy in a long and dark winter. Here, in this study, we investigated the annual transcriptome response of extremophile plants in a natural environment. During the 2015-2016 winter/summer station study, we had sampled *Sanionia uncinata*, one of the dominant bryophyte species of the maritime Antarctic, naturally habituated in the King George Island (62°14′ S; 58°44′ W), on a monthly basis, and conducted transcriptome analysis. As a result, we could identify groups of genes that fluctuate with rhythmicity according to the seasonal changes. The weighted co-expressed gene network analysis enabled to construct a correlation network on climate-gene expression and to identify the groups of genes responding to changing climatic factors in a natural environment.

Keywords: Environmental adaptation, Field transcriptome, *Sanionia uncinata*, Antarctica,
De novo genome assembly of *Sanionia uncinata* (Amblystegiaceae: Hypnales), a pleurocarpous moss dominant in Antarctica

Hyoungseok Lee$^{1,2}$, Hyun Park$^{1,2}$, Mi Young Byun$^1$, Mira Park$^1$, Jungeun Lee$^{1,2}$

$^1$ Unit of Polar Genomics, Korea Polar Research Institute, Incheon 21990, South Korea (soulaid@kopri.re.kr); $^2$ Polar Science, University of Science & Technology, Incheon 21990, South Korea

Mosses in Antarctica grow mostly in coastal areas and are expected to have developed various unique physiological/molecular mechanisms to survive in extreme environments. *Sanionia uncinata* (Hedw.) Loeske (Amblystegiaceae: Hypnales) is a dominant moss species in the maritime Antarctic and considered as a good target to investigate genes associated with abiotic stress tolerance of mosses. It has several distinct characteristics when compared to *Physcomitrella patens*, the first model moss species. First, *S. uncinata* is a pleurocarpous moss. Second, it belongs to the order Hypnales which contains the largest number of species in the moss phylogeny. Third, it is an alpine species that lives in cold regions unlike *P. patens* mostly found in temperate regions. Here, we report the draft genome sequence of an Antarctic *S. uncinata*, obtained using third-generation PacBio sequencing technology. About 1 million reads were attained from four Sequel sequencing runs and merged together into a single dataset of 21 Gb. The *de novo* assembly produced 673 contigs comprised of 621 Mb with an N50 contig length of 2.2 Mb and the longest contig length of 10.3 Mb, and a total of 28,651 coding genes were inferred. When the completeness of the genome was assessed by BUSCO analysis with the Eukaryota odb9, *S. uncinata* draft genome showed 91.1% complete, 0.3% fragmented, and 8.6% missing BUSCO. Our dataset can be used as a comparative genome for evolution and speciation studies for bryophytes, as well as for the analysis of molecular adaptation of plants to harsh environment.

**Keywords:** Antarctica, genome, Hypnales, *Sanionia uncinata*
Phylogenomic analyses of ancient sex chromosomes in *Ceratodon purpureus* highlight the dynamism of sexual systems in bryophytes

Stuart F. McDaniel1, Sarah B. Carey1, and the Ceratodon Genome Consortium2

1 Department of Biology, University of Florida, Gainesville, FL 32611 U.S.A. (stuartmcdaniel@ufl.edu); 2DOE Joint Genome Institute, Walnut Creek CA, 94598, U.S.A. and numerous collaborators

Sex chromosomes have evolved several times across the tree of life, yet the evolutionary processes shaping their gene content remain enigmatic. Sex-chromosomes are well-documented in bryophytes, providing an untapped resource for exploring factors shaping the evolution of sex-chromosome gene content and chromosomal architecture. Sex in dioecious bryophytes is determined by a UV sex chromosomal system. In this system, each sex has a non-recombining chromosome (U for females and V for males). The U and V pair at meiosis in the monomorphic diploid sporophyte and segregate to the haploid male and female gametophytes. Because the sex chromosomes are transcriptionally active in the haploid stage, and therefore subject to purifying selection, we expect many orthologous genes will be retained between the U and V chromosomes. Here we use a combination of Illumina, PacBio, and Hi-C sequence data to generate chromosome-scale assemblies of the 360 megabase (Mb) genomes of a male and a female isolate of the moss *Ceratodon purpureus*. We used genes annotated on the ~100Mb U and V sex chromosomes of *C. purpureus* and existing transcriptome data of other moss species to study the evolution of gene content and chromosome architecture of moss sex chromosomes. These analyses demonstrate that the moss sex chromosomes evolved in the ancestor of nearly all mosses (~300mya) or even may predate the origins of the bryophytes, contradicting earlier results based on ancestral reconstructions of the bryophyte sexual system. Interestingly, the sex chromosomes contain several conserved transcription factor families, with important roles in sexual differentiation across the green plants. In spite of this conservatism, the phylogenomic analyses also show that both the U and V have continued to acquire genes over time, and that the genetics of sexual dimorphism are highly dynamic.

Keywords: Sex chromosome, genomics, transcription factor, molecular evolution, dioecy
Expanded delimitation of *Physcomitrium* (Funariaceae) based on targeted sequencing of nuclear exons and their flanking regions

Rafael Medina¹, ², Matthew G. Johnson³, ⁴, Yang Liu¹, ⁵, Norman J. Wickett³, A. Jonathan Shaw⁶ & Bernard Goffinet¹

¹ Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, U.S.A. ² Department of Biology, Augustana College, Rock Island, IL 61201, U.S.A. (rafaelmedina@augustana.edu) ³ Chicago Botanic Garden, Glencoe, IL 60022, U.S.A. ⁴ Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, U.S.A. ⁵ Shenzhen Fairy Lake Botanical Garden, Shenzhen 518004, China. ⁶ Department of Biology, Duke University, Durham, NC 27708, U.S.A.

The architecture of the sporophyte and its spore dispersal mechanisms are a key feature in the evolution and systematics of mosses. Since the selection pressure related to these mechanisms is assumed to be critical in the phylogenetic history of these plants, the loss of sporophytic complexity constitutes a relevant topic of study in moss evolution. The Funariaceae is an optimal commonplace to study sporophyte evolution since this family exhibits variable sporophyte complexities, spanning from long, exerted, operculate capsules with two rings of well-developed teeth, to capsules immersed and completely cleistocarpous. Recent independent studies have confirmed that the family underwent a rapid diversification, but the relationships of taxa with reduced sporophytes and the major genera *Entosthodon* and *Physcomitrella* remained ambiguous. We inferred the relationships of a selection of 70 Funariaceae accessions, including five taxa with highly reduced sporophytes, using 648 nuclear loci (exons complemented by their flanking regions), based on inferences from concatenated data and concordance analysis of single gene trees. *Physcomitrellaopsis* is resolved as nested within one clade of *Entosthodon*. *Physcomitrella* s. lat., is resolved as a polyphyletic assemblage and, along with its putative relative *Aphanorrhegma*, nested within *Physcomitrium*. We propose a new monophyletic delineation of *Physcomitrium*, which accommodates species of *Physcomitrella* and *Aphanorrhegma*. The monophyly of *Physcomitrium* s. lat. is supported by a small plurality of exons, but a majority of trees inferred from exons and their adjacent non-coding regions.

Keywords: Cleistocarpy, *Entosthodon*, *Physcomitrium*, *Physcomitrella*, Phylogenomics
High efficient and precise base editing in Physcomitrella patens genome using modified CRISPR/Cas9 systems

Fabien Nogué1, Anouchka Guyon-Debast1, Zoé Terret2, Florence Charlot1, Jean-Luc Gallois2,

1Institut Jean-Pierre Bourgin, INRA, AgroParisTech, CNRS, Université Paris-Saclay, 78000 Versailles, France (fabien.nogue@inra.fr); 2 GAFL, INRA, Montfavet, France

The moss Physcomitrella patens is now a well established model organism for studying conserved signalling pathways and developmental processes during plant evolution. Its short life cycle, ease of cultivation, and high rate of gene targeting have made it an ideal system for genetic analysis. However, the fact that this moss is haploid and the difficulty of isolating hypomorphic mutants can limit gene function analysis. We have already demonstrated the potential of the CRISPR-Cas9 system for targeted gene knock-out in this plant. Here we developed in P. patens an efficient method for targeted base editing, a form of genome editing that enables direct, irreversible conversion of one base pair to another at a target genomic locus without requiring double-stranded DNA breaks (DSBs). For this purpose we used two different base-editing constructs. The first one consists in a nickase CRISPR/Cas9 (nCas9) fused to Petromyzon marinus cytidine deaminase (PmCDA1) and can lead to C→T, C→A, C→G substitutions. The second one consists in a nickase CRISPR/Cas9 (nCas9) fused to an engineered Escherichia coli transfer RNA adenosine deaminase (ecTadA) that can operate on DNA and lead to A→G substitutions. As a proof of concept we designed Single-guide RNAs (sgRNAs) to target an endogenous reporter gene, PpAPT, whose inactivation confers resistance to 2-fluoroadenine. Transformation of moss protoplasts with these sgRNAs and the base-editing constructs triggered mutagenesis at the PpAPT locus in about 1.8% of the regenerated plants (64% of the transfected plants). In addition we could show in this study that the base-editing system is very efficient for multiplex base editing as we were able to modify bases in four regions of the same gene simultaneously. In one experiment we could obtain 31 variants of the APT protein that gave us original information on important amino acids/peptides for this enzyme, showing the potential of these newly developed CRISPR-Cas base editors for gene function analysis in P. patens.

Keywords: Gene editing, CRISPR-Cas9, APT, gene function analysis
Information for submission of abstracts to the Bryology 2019 meeting. Deadline: 31 May 2019

**Presentation type:** Oral Presentation, Poster Presentation

**Abstract Title:** A Trans-kingdom Myosin XI Interaction with a RabE GTPase is Essential for Polarized Growth

Robert G. Orr1, Fabienne Furt1, Erin Warner1, Erin M. Agar1, Jennifer Garbarino1, Sarah E. Cabral1, Michelle L. Dubuke2, Allison M. Butt1, Mary Munson2, and Luis Vidali1

1Dept. of Biology and Biotechnology, Worcester Polytechnic Institute, Worcester, MA 01609 (rorr@wpi.edu); 2Dept. of Biochemistry and Molecular Pharmacology, University of Massachusetts Medical School, Worcester, MA 01605

The fundamental eukaryotic process of intracellular trafficking requires the interconnected activity of molecular motors trafficking vesicular cargo within a dynamic cytoskeletal network. However, in plants, few mechanistic details are known about how molecular motors associate with their secretory cargo to support the ubiquitous processes of polarized growth and cell division. A yeast two-hybrid screen of a *Physcomitrella patens* library identified a RabE GTPase as an interactor of myosin XI and subsequently demonstrated all five RabE members interact with myosin XI. Consistent with a role in polarized transport, we observed RabE at the growing cell apex and at the expanding cell plate during cell division. An *in vivo* cross-correlation analysis of fluorescently tagged RabE and myosin XI revealed that both species are spatiotemporally coupled, demonstrating their simultaneous involvement in polarized growth. To determine if myosin XI and RabE are directly coupled, we first computationally predicted myosin XI:RabE interface through a homology modeling-directed approach. We identified a structurally conserved residue on myosin XI, V1422, that when mutated abolished RabE binding in the yeast two-hybrid system and resulted in unpolarized plants instead of the characteristic network of filamentous cells when regenerated from single cells. Directed yeast two-hybrid using the cargo-binding domain of myosin XI-K from *Arabidopsis thaliana* demonstrated a direct interaction with RabE from *P. patens*. Furthermore, chimeric myosin XIs comprised of cargo-binding domains from *A. thaliana* successfully rescued growth in a silenced myosin XI moss background. Together, this work demonstrates the requirement of a direct myosin XI:RabE interaction for polarized growth in plants.

**Keywords:** intracellular trafficking, tip growth, cytoskeleton, myosin XI, Rab GTPase
The first high-quality reference genome for hornworts (Anthoceros) reveals drastically different genome structure from those of mosses and liverworts.

Péter Szövényi, Fay-Wei Li, Tomoaki Nishiyama, Keiko Sakakibara, Juan-Carlos Villareal, Mareike Schallenberg-Rüdiger, Stefan Rensing, Anna Neubauer, Manuel Waller, Alexander Kirbis, Seydina Issa Diop

1University of Zurich, Switzerland (peter.szoevenyi@uzh.ch); 2Cornell University, USA; 3Kanazawa University, Japan; 4Rikkyo University, Japan; 5Laval University, Canada; 6University of Bonn, Germany; 7University of Marburg, Germany

The monophyletic group of hornworts is believed to represent the immediate sister group of all vascular land plants. However, this traditional view is still debated and cannot be satisfactorily resolved owing to the lack of detailed knowledge on the general biology and genomic features of hornworts. Until now, advancement in this field was primarily hindered by the lack of genomic resources for a hornwort model species.

Here we provide a high-quality genome draft of the model hornwort, Anthoceros agrestis, and some of its relatives. With the aid of Chicago and Hi-C libraries we assembled the A. agrestis genome into 5-6 chromosomes spanning a total length of ca. 120 Mb.

The A. agrestis genome drastically differ from the published bryophyte genomes (moss and liverwort) and exhibit a number of unique features. The A. agrestis genome is small and strongly streamlined. In particular, we show that it has few recent paralogs, exhibits no signs of whole-genome duplication and has a moderate repeat content (ca. 30%). Despite of its small size, the genome is densely packed with genes (28 000 genes) of which 30% seems to be unique to hornworts showing no homology to genes of land plant and green algal genomes. We further show that the genome contains over 3000 PPR genes (pentatricopeptide repeat) known to be involved in organellar RNA editing that is pervasive in chloroplast-derived transcripts of A. agrestis. Finally, we present a preliminary gene expression atlas which shed light on the regulation of morphological and developmental traits that are either shared with other embryophytes or unique to hornworts.

Overall, our analysis suggests that the hornwort genome is radically different from that of other land plants. Its unique and shared features within land plants provides better understanding on the evolutionary genomic events accompanied the origin and evolution of land plants.

Keywords: hornworts, land plants, genome size, symbiosis, RNA editing
The genome of the moss *Funaria hygrometrica* provides insights into chromosomal-scale genome evolution in Funariid mosses.

Peter Szovenyi¹, Yang Liu²,³, Nasim Rahmatpour³, Alexander Kirbis¹, Manuel Waller¹, Jill Wegrzyn⁴, Bernard Goffinet⁴

¹University of Zurich, Switzerland (peter.szoevenyi@uzh.ch); ²BGI-Shenzhen, China; ³Fairylake Botanical Garden, China; ⁴University of Connecticut, USA;

Thanks to its attractive phylogenetic position and molecular genetic attributes the model moss *Physcomitrella patens* has become a powerful tool for developmental and molecular genetic research during the last decade. Although many of the advantageous properties of the bryophyte system have been used in studies on development and cellular function, several peculiar characteristics have not received much attention so far. In particular, evolutionary genomics and comparative developmental genomics of mosses are still in their infancy and are waiting to be exploited.

Here we report the genome of *Funaria hygrometrica*, a relative of the model moss *P. patens*. *Funaria* and *Physcomitrella* represent end points of morphological and developmental complexities (complex and reduced sporophyte morphology in *Funaria* and *Physcomitrella*, respectively) within the group of Funariid mosses thus providing an ideal model system for comparative studies.

Using a polished PacBio assembly and additional Chicago and HiC libraries we present our genome assembly consisting of 26 chromosomes with a total length of ~320 Mb.

We show that many features of the *F. hygrometrica* genome are shared with those of *P. patens* but some striking differences exist with strong phenotypic consequences. The two genomes have largely co-linear chromosomes, share 20 000 orthologous genes and two whole-genome duplications. Despite these similarities, the *Funaria* genome is approx. 160 Mb smaller which is associated with the preferential loss of repetitive DNA. It also contains more than 8000 *Funaria*-specific genes preferentially expressed in the complex sporophyte phase. We also show that the *Funaria* karyotype consisting of 26 chromosomes can be easily derived from the 27 chromosomes of *P. patens* via two chromosome fusions and one fission.

Overall, our data provides insights into how loss of repetitive DNA, chromosome fusions/fissions and gene losses/gains have contributed to the evolutionary and morphological divergence of the *P. patens* and *F. hygrometrica* genomes.

Keywords: genome evolution, land plants, genome size expansion, sporophyte, gene number
The monophyly of Bryophytes is supported by nuclear and plastidial protein phylogenies

Filipe de Sousa¹, Cymon J. Cox¹

¹Centro de Ciências do Mar, Universidade do Algarve, Gambelas, 8005-319 Faro, Portugal (filipedeportugal@gmail.com)

Determining the phylogenetic relationships among the first land plant lineages is essential for an understanding of the evolution of terrestrial ecosystems. The predominant point of view has been that bryophytes were the first to colonise land and that tracheophytes descend from an ancestral bryophyte. This hypothesis is supported by molecular evidence, including organellar and nuclear protein-coding genes. However, analyses of the amino acid translation of these same data show an alternative pattern whereby mosses and liverworts form a group that often includes hornworts. We show that the signal supporting the hypothesis of a bryophyte ancestor of land plants is mostly driven by substitutional saturation at synonymous sites in nucleotide data, and that non-synonymous sites and amino acid nuclear data converge on the same supported result, namely, that bryophytes form a monophyletic group. These results indicate that conventional stationary substitution models are inadequate for analyses of molecular data that is highly saturated and affected by composition bias. Analyses of codon-degenerate and amino acid-translated nuclear and chloroplast data, under composition tree-heterogeneous models, strongly support the monophyly of bryophytes, and imply that an ancestral land plant lineage diverged rapidly into bryophytes and tracheophytes. This relationship suggests that the bryophyte life-cycle, characterised by a dominant gametophyte that nurtures an unbranched sporophyte, is not ancestral to all land plants, and that stomata are a symplesiomorphy among all land plants.

Keywords: land plants, bryophytes, phylogeny, molecular evolution, composition bias
Geometric cues forecast the switch from 2D-to-3D growth in *Physcomitrella patens*

Han Tang\(^1\), Kilian Duijts\(^2\), Magdalena Bezanilla\(^4\), Ben Scheres\(^1\), Joop E.M. Vermeer\(^3\), and Viola Willemsen\(^1\)

\(^1\) Laboratory of Plant Developmental Biology, Wageningen University & Research, Wageningen, The Netherlands  
\(^2\) Laboratory of Cell Biology, Wageningen University & Research, Wageningen, The Netherlands  
\(^3\) Plant Cell Biology, Department of Plant and Microbial Biology and Zurich-Basel Plant Science Center, University of Zürich, 8008 Zürich, Switzerland  
\(^4\) Biological Sciences Department, Dartmouth College, Hanover, NH, USA

Asymmetric cell divisions, in which a daughter cell acquires a new identity, are crucial for plant growth and development throughout evolution. The successful colonization of land by the basal plant *Physcomitrella patens* was achieved by a critical switch in its growth pattern, facilitated by an asymmetric division that initiates a bud from a filamentous cell with gametophore identity. Insights into the underlying mechanisms coordinating this switch are still unknown. By 2D-, 3D-imaging and image segmentation, we identified and quantified two geometric cues, the width of the initial cell and the angle of the transition division plane, which sufficiently distinguished a gametophore initial cell from a branch initial cell. These identified cues were further confirmed in bud-enriched and bud-deficient mutants, respectively. The identification of a fluorescent marker allowed us to successfully predict the gametophore initial cell with more than 90% accuracy. This high prediction accuracy confirms our hypothesis that before the asymmetric cell division, parental cells of the gametophore initials already possess different cellular properties compared to branch initials. Our results indicate that the cell fate decision of the daughter cell is determined in the parental cell, prior to the completion of the cell division.

**Key words:** 2D-to-3D development, cell fate switch, asymmetric cell division, geometric cues, *Physcomitrella patens*
Genetic pathways controlling meristematic activity and differentiation in hornwort-sporophytes

Manuel Waller¹, Alexander Kirbis¹, Anna Neubauer¹, Ana Marcela Florez Rueda², Ueli Grossniklaus³, Péter Szövényi¹

¹Department of Systematic and Evolutionary Botany, University of Zurich, Zürich, Switzerland (manuel.waller@uzh.ch); ²Department of Plant and Microbial Biology, University of Zurich

A major change that accompanied the evolution of embryophyte land plants from a haplontic ancestor was the elaboration of the sporophyte and parallel reduction of the gametophyte phase. Flowering plants have established complex branched sporophytes, which grow through the continuous activity of a multicellular meristem located at the tip of the shoot. Genetic developmental pathways controlling the activity of this shoot apical meristem have been extensively studied in flowering plants, most notably of A. thaliana and Z. maize. In contrast, bryophytes, the most basal group of extant land plants, have subordinate, unbranched, monosporangiate and upright sporophytes that remain attached to the gametophyte generation. Bryophyte-sporophytes exhibit multicellular meristems that contribute to sporophyte growth, referred to as intercalary meristem in mosses and basal meristem in hornworts. Yet, regulatory mechanisms controlling the activity of these bryophyte-meristems are not known. Comparison of regulatory gene networks controlling sporophyte development in bryophytes and vascular plants will help resolving the evolutionary-developmental trajectory between bryophyte-sporophytes and the more complex sporophytes of vascular plants. Therefore, our main goal is to provide a detailed account on the regulatory mechanism governing sporophyte development in bryophytes. To this end, we established transcriptomic profiles for five different sporophyte tissues of the hornwort Anthoceros agrestis, using laser-assisted microdissection coupled with RNA-sequencing. Analysis of differential gene expression across these five tissues allows us to establish a hypothetical model of regulatory mechanisms involved in governing sporophyte development in hornworts. Additional comparison of this transcript dataset with data available for the P. patens gametophytic apical cell and sporophyte, as well as the SAM of Z. maize, enables us to refine hypotheses regarding the evolutionary relationship of multicellular meristems of land plants. Future work will focus on describing fine-scale spatial expression of proposed candidate genes and testing their functional role using reverse genetic approaches.

Keywords: hornworts, sporophyte development, sporophyte evolution
**Presentation type:** Oral Presentation, Poster Presentation (underline the preferred type)

**DNA double strand break (DSB) repair in protonema tissue of the moss *Physcomitrella patens***

Karel J. Angelis, Radka Vágnerová, Marcela Holá

The Czech Academy of Sciences, Institute of Experimental Botany, Na Karlovce 1, CZ-16000, Prague, Czech Republic (karel.angelis@gmail.com)

Protonema of the moss *Physcomitrella patens* is a unique tissue, which with regard of cultivation conditions enables to study tissue either with majority of cells in chloronema arrested at G2/M stage or that of caulonema arrested at G1/S stage. The objective of this study was to study differences in response of these tissues to DSBs induced by bleomycin. Subculturing of protonema generates fragments of 3-7 cell of which up to 50% are apical, whereas 7 days after subculture, fragments extend, often branch, and only fraction of cells is apical. By weighting explants, primary caulonema and chloronema showed to be more resistant to 1 hour bleomycin treatment than 7 day grown tissue and, as estimated by comet assay, also more efficiently repair DSBs. Same differences between primary and 7 day tissue are also among lines mutated in SOL, NSE1 and NSE4. SOL is a homologue of *Arabidopsis* SOG1 transcription factor that controls response to gamma irradiation. Its mutation allows the cell-cycle progression manifested as a phenotype resistant to bleomycin and efficient DSB repair when compared to wt. Contrary to SOL, NSE1 and NSE4 are essential kleisin genes of SMC5/6 complex, which in circular form stabilizes DSB during repair. The viable CRISPR/dCas9 nse1 and nse4 lines show very similar phenotype with sol line. We conclude that in primary tissue the rate of DSB repair is extremely efficient regardless of SOL or NSE1, 4 mutations, whereas much slower in older tissue, suggesting that repair is not so urgent for cell survival as in dividing cells. When replication is not a primary need for cell survival, more elaborate mechanisms of repair start to be involved and lead to ambiguous repair kinetics.

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**Keywords:** Tissue differentiation, sensitivity to DSB induction, mechanism and kinetics of DSB repair, CRISPR/dCas9 mutants
Effect of air pollution on species composition of communities of epiphytic bryophytes with respect to bark chemistry

Jana Procházková¹, Eva Mikulášková¹, Tomáš Hájek², Vítězslav Plášek³ & Michal Hájek³

¹Department of Botany and Zoology, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic (jana.prochazkova@mail.muni.cz); ²Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic; ³Department of Biology and Ecology, University of Ostrava, Chittussiho 10, 710 00 Ostrava, Czech Republic

Epiphytic bryophytes are susceptible to air pollution. Disappearance of sensitive species from highly polluted areas and their return after decrease of pollution load was recorded during the second half of the 20th century in Europe as well as in recently polluted industrial areas. However, effect of air pollution on epiphytic communities composition and the associated role of host tree bark chemistry has not been sufficiently explored. The main aim of our study was to assess the effect of air pollution on the structure of epiphytic bryophyte communities hosted by tree species with different bark pH. Due to higher buffering capacity of basic substrates, we expected smaller difference between communities on host trees with higher bark pH in areas with distinct pollution loads. Epiphytic bryophytes were studied on 50 study sites with similar climatic conditions but contrasting levels of air pollution (based on model data of SO₂ and NOₓ loads) in Central Europe. All species of bryophytes and their abundances were recorded on the five trunks of oaks (Quercus robur or Q. petraea, lower bark pH expected) and five ashes (Fraxinus excelsior, higher pH expected) from the ground to 2 m height at each study site. Additionally, four phytosociological relevés 25 × 25 cm were recorded on all trees. As a proxy for the current pollution load at each site, thallus N concentration was measured in Hypnum cupressiforme or H. andoi. We recorded 89 species of bryophytes in total. Epiphytic communities are more species-rich in areas with low levels of air pollution both on oaks and ashes. Air pollution was found to be a significant environmental variable explaining part of variability among studied communities. Bark pH and N concentration in Hypnum thalli corresponded to model data of SO₂ and NOₓ loads. Bark pH range was shorter on ashes, acidifying impact of pollution was buffered partially. Species composition of communities on ashes differed only under the highest SO₂ load, on the contrary, oak communities were affected by high level of any pollutants as the bark become more acidified. Air pollution thus determines the structure of epiphytic bryophytes communities.

Keywords: epiphytic bryophytes, epiphytic communities, air pollution, host tree bark pH
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**The ratio between bryophyte functional groups impacts vascular plants in rich fens**

Patrícia Singh 1, Jakub Tešitel 1, Zuzana Plesková 1, Tomáš Peterka 1, Daniel Dítě 2, Petra Hájková 1,3, Pawel Pawlikovski 4, Michal Hájek 1

1 Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-611 37 Brno Czech Republic

2 Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Dúbravská cesta 9, 18 SK-845 23, Bratislava, Slovakia

3 Laboratory of Paleoecology, Institute of Botany, The Czech Academy of Sciences, Lidická 25/27, CZ-602 00 13 Brno, Czech Republic

4 Department of Plant Ecology and Environmental Conservation, Faculty of Biology, Biological 9 and Chemical Research Centre, University of Warsaw

Fens have well-developed bryophyte layer covering most of the ground. Non-sphagnaceous bryophytes, especially the group of so-called brown mosses, prevail over sphagna under alkaline conditions. In sub-alkaline conditions, rich fens allow the co-occurrence of these both functional groups, but sphagna are competitively superior over non-sphagnaceous bryophytes and seedlings of vascular plants, and they are currently expanding in some regions. We test whether the ratio between the two major bryophyte functional groups (*bryo-ratio*) accounts for species composition of fen-specialized vascular plants.

We analyzed two datasets of the vegetation-plot records by Canonical Correspondence Analysis with variation partitioning (community-level analysis) and Structural Equation Modelling (species-level analysis).

At the community level, the *bryo-ratio* accounted significantly for species composition of fen-specialized vascular plants. At the species level, most of the species affected significantly by the *bryo-ratio* preferred the fens rich in non-sphagnaceous bryophytes. They were largely those with a low capability of vegetative reproduction.

Species preferring brown moss patches include mostly rare and endangered species with a great need for generative reproduction (e.g., *Primula farinosa*, *Triglochin palustris*, *Pedicularis palustris*, *Saxifraga hirculus*). We demonstrate the important role of the bryophyte layer in the structuring of vascular plant communities in fens and highlight urgent conservation needs for brown moss patches.

**Keywords:** Brown mosses, sphagna, endangered species, diversity hotspots, mires, conservation ecology
Molecular phylogenetic studies of mosses revealed two terminal clades, the subclasses Bryidae and Dicranidae, largest in number of species, and the grade leading to them from primarily eperistomate and nematodontous groups through Buxbaumiidae, Diphysiidae and Funariidae. Buxbaumiidae and Diphysiidae have highly specialised peristomes, not splitting into definite number of separated elements. The three subclasses, Funariidae, Bryidae and Dicranidae are characterized by three main peristome types: diplolepideous opposite, haplolepideous, and diplolepideous alternate respectively, and this correlation is a fundamental fact of the backbone moss system. The recent anatomical studies of the peristome development, however, challenge some its aspects: (1) origin of the *Diphyscium* peristome type from the *Buxbaumia*-type; instead *Buxbaumia* is likely a derivative from *Diphyscium*-like ancestor; (2) the occurrence of diplolepideous peristomes in some groups of Dicranidae (which are commonly called just "haplolepideous"); (3) The opposite position of elements of endostome and exostome may repeatedly appear as a kind of peristome reduction, thus Funariidae may be assumed not as one of three basic peristome types, but a side lineage, representing several variants of strongly modified peristome types.

Keywords: anatomy, morphogenesis, Funariidae, Bryidae, Dicranidae, Buxbaumia
Are all paraphyllia the same?

Ulyana N. Spirina¹,², Tatiana V. Voronkova², Michael S. Ignatov²,³

¹Tver State University, Zhelyabova St. 33, Tver, 170100, Russia (ulayspirina@mail.ru); ²Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str. 4, Moscow, 127276, Russia; ³Lomonosov Moscow State University, Biological Faculty, Geobotany Dept., Leninskie Gory Str. 1-12, Moscow, 119234, Russia

Paraphyllia and pseudoparaphyllia are two terms which are important in pleurocarpous mosses systematics, yet their misapplication continues. Paraphyllia are treated as adventive structures (appendages) of stem epidermis, in contrast to foliose or filamentose structures around branch primordia commonly referred to the pseudoparaphyllia. One of the reasons for that misapplication is the neglected fact that proximal branch leaves are often not only incised, but sometimes subdivided up to the base, and moreover, their parts might occur spaced from each other to a certain distance, looking as independent subfilamentose structures, which we called compound leaves. Especially puzzling are cases, when compound proximal branch leaves appear around undeveloped branch primordia. These leaves apparently belong to “virtual branch” as they have clear phyllotaxis, as e.g. Leskea and Cratoneuron, The branch apical cells in this case appear to be hidden almost totally under the stem epidermis. Such filamentose parts of compound branch leaves we suggest to call Leskea-type paraphyllia. There are at least two cases where paraphyllia have likely a different type. In genera with papillose stem, e.g. Pelekium, there are transitions from unicellular to multicellular raisings on each cell of the stem surface, pointing thus the homology with papillae, comprising Pelekium-type paraphyllia. The third, Climacium-type paraphyllia is observed in Climacium and Pleuroziopsis. In this case paraphyllia occur in longitudinal rows along the stem, without any connection to primordial, and possess many characters of rhizoids. New observations in anatomy allow circumscribe Leskea-type of paraphyllia in details, revealing facilitation its development by exogenous ABA application.

Keywords: paraphyllia, pseudoparaphyllia, compound leaves, ABA