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The phylogeny, biogeography, and ecology of the moss Syntrichia (Brid.)

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The phylogeny, biogeography, and ecology of the moss *Syntrichia* (Brid.)

By

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requirements for the degree of

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of the

University of California, Berkeley

Committee in charge:

Professor Brent D. Mishler, Chair
Professor Paul V. A. Fine
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Abstract

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In the midst of global climate change, it is crucial to understand the spatial patterns of biodiversity and its underlying ecological and evolutionary mechanisms, including neglected groups in the tree of life such as bryophytes (liverworts, mosses, and hornworts). These lineages share some important characters with tracheophytes (e.g., embryonic development and elaboration of the sporophyte generation), but also, they have retained characters from their freshwater algal ancestors (e.g., desiccation tolerance, poikilohydry, and dominant gametophyte). Because of their unique biology, they are ideally suited for addressing questions in evolutionary biology, functional morphology, and biodiversity.

This Dissertation consists of three independent but interconnected topics using mosses as a study system. In Chapter 1, I aim to understand the patterns of diversity and community structure of mosses along elevation and moisture gradients in Central Chile. Chapter 2 addresses the evolutionary history of the dryland moss *Syntrichia* Brid. Chapter 3 focuses on functional morphology in relation to external water-conduction in *Syntrichia*.

The goal of Chapter 1 was to investigate the diversity of mosses along an elevational gradient in Central Chile. I used phylogenetic approaches (phylogenetic diversity, relative phylogenetic diversity, and phylogenetic turnover) to measure the diversity and community structure of 25 sites along an elevation gradient in Central Chile. To understand the composition of moss communities according to soil moisture, each site was subdivided into three subsites arranged perpendicularly to a water source (e.g., creek) ranging from completely dry to fully moist. The phylogenetic pattern suggested that environmental filtering was responsible for the co-occurrence of closely related taxa at low and high elevations, and that competition had a minimal effect on community assembly. Phylogenetic turnover revealed changes in community composition along elevation and soil moisture.

In Chapter 2, I aimed to investigate the evolutionary, biogeographic history, and trait evolution of *Syntrichia*, through the most comprehensive phylogenetic analysis performed up-to-

date. A combined phylogeny based on a hundred nuclear loci plus a robust morphological matrix suggested that *Syntrichia* is monophyletic with 10 major subclades. It is very likely *Syntrichia* originated in South America in the early Eocene and dispersed to other landmasses via dispersal. The genus experienced major diversification events in South America and Northern Hemisphere, the areas with the current greatest species diversity. Habitat preferences (e.g., soil, rocks, and trees) might be associated with evolutionary changes in water-related traits.

Chapter 3 explored how the moss *Syntrichia* absorbs, conducts, and retains water externally, a process known as ectohydry. I used a diverse range of microscopic techniques for observing anatomy as well as experimental approaches to understand the rate of conduction and dehydration. I propose a new framework for studying ectohydric capabilities that include three spatial scales (cell anatomy, stem architecture, and whole clump) and timing to become fully hydrated. There was a trade-off between speed of conduction and holding capacity that could be associated with the life history of each species.

This dissertation is a contribution to the understanding of several fundamental questions in the biology of mosses. This work will provide the basis for future research in the field of evolution, ecology, and functional morphology.

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Preface

When I was an undergraduate student in Chile, I asked myself whether all the plants on Earth have flowers. Since I was studying the physiology of fruits, the word "fruit" was a given term in class without recognizing its biological and evolutionary significance. This question remained unanswered for a long time until I decided to study abroad at the University of California, Davis. There, I met Dr. D. Potter and J. Doyle who showed and taught me the beauty of the evolution of angiosperms. While I could answer my primary question, I began a new inquisitiveness. What do the relatives of angiosperms look like? Do these plants have a more 'primitive' lifestyle and simpler reproductive structures than angiosperms? Are these plants co-occurring with angiosperms? Given that my curiosity was active and beating, I decided to fill a gap in knowledge by choosing an unexplored group, yet important to understand the biology and evolution of land plants.

The world of mosses, liverworts, and hornworts, commonly known as bryophytes completely fulfilled my expectations. Despite these plants being often overlooked due to their small size and lack of attractive flowers, they form a miniature forest that has a crucial role in our environment. They serve as colonizers of disturbed soils and prevent soil erosion[1], participate in nutrient cycling[2], provide shelter for many invertebrates[3], and absorb and gradually release water back into the ecosystem to promote the germination of new plants[4]. Their global diversity (~20,000 named species) is by far superior to other groups of plants, such as ferns or gymnosperms[5,6], and surprisingly they could survive in rocks, walls, and city pavements, where most other plants are excluded!

Still, there is much to learn about bryophytes, especially in dryland ecosystems. Commonly, people associate bryophytes with damp or shady habitats, however, they also can thrive in extreme habitat conditions, such as deserts or the antarctic. In these harsh ecosystems, they are able to flourish two of the most remarkable, but less known traits in plants: *desiccation tolerance* and *poikilohydry*. These two traits are complementary but really distinct from each other. With the first trait, a moss can suspend its metabolism when dry - become completely dead looking - and rapidly resume photosynthesis and growth during moist periods[7]. Given their poikilohydric lifestyle, on the other hand, these plants have a more intimate relationship with the environment. They absorb water directly from their surroundings[8]. In other words, when they are dried, they could easily absorb moisture in the form of dew or fog from the atmosphere[9].

From an evolutionary standpoint, these plants are thought to be the closest relatives of the first terrestrial plants. It is very likely that the first land plants inherited some characteristics from freshwater algae ancestors[10]. Bryophytes retained some of these ancestral characters, such as desiccation tolerance and flagellate sperms, but also shared some characters with all other land plants (e.g., development of the embryo and elaboration of a sporophyte generation)[11]. They also have been subjected to the same evolutionary forces as other groups. They show local adaptations to natural selection, have dynamic biogeographic patterns, complex evolutionary history of hybridization, and the creation of morphologically cryptic lineages[12]. Therefore, they can reveal

essential information about how the first plants adapted to terrestrial environments, but also inform how evolution has shaped their current diversity. Thus, we cannot fully understand the complex function of structures and diversity of angiosperms without a sense of history that includes bryophytes in their pivotal piece in the transition from freshwater to land habitats.

This dissertation started from a commonplace curiosity. I believe that each species has its role in nature, then each species needs special attention when talking about biodiversity. That is the main reason why I decided to study the biodiversity pattern in bryophytes in a very specific area. In Chapter I, I aim to address the diversity pattern using traditional and phylogenetic metrics along an elevational gradient in Central Chile. One of the transects involved a route that we used to do with my friends that ends with a gratifying waterfall. I wanted to know whether mosses were living in these harsh conditions. If so, are they isolated or co-occurring with other species? After polishing these questions, I finally evaluated the diversity levels under a phylogenetic and community framework.

A recurrent moss that I found during my field trips in Chile is *Syntrichia.* This moss has remarkable levels of diversity, broad ecological tolerance, and great morphological disparity compared to its closest relatives[13]. Despite being considered as a taxonomically complex group, I took the challenge of investigating its evolutionary and biogeographic history. In addition, Brent has been pushing to know the history of this group since early on during his Ph.D. In Chapter II, I wanted to investigate and understand the global history of this group sampling most of the species worldwide. I also wanted to know whether the Andes in South America had any implications for shaping the current disjunct distribution among continental landmasses.

Despite the typical relegation to the category of non-vascular plants, water conduction and storage have played major roles in bryophytes[14,15]. However, instead of using an internal machinery for the conduction of water from the soil to the canopy, mosses evolved a new strategy in response to their poikilohydric lifestyle. They can absorb, conduct, and retain water externally, a phenomenon known as *ectohydry*[16]. In Chapter III, I aim to link the anatomical and morphological aspects of the moss with functional capabilities using *Syntrichia* as a model system to study ectohydry. *Syntrichia* is a masterpiece for this purpose. Just observing how a dried moss clump reacts to a small drop of water and their fast reaction is enough to note they are physiologically active. Here we re-confirm that moss biology is fascinating!

I hope this dissertation, and its following publications, are a source of inspiration for new students that want to investigate something that could start at the level of curiosity, followed by a scientific methodology. Today a thesis rooted purely in natural history is scarce, but tremendously important to set new foundations in organismal biology. Basic science in biology tries to understand the natural world without the expectation to solve a particular problem. We must remember that some of the major contributions of science to society come from doing basic science. The discovery of the first human cancer gene, the first chemical synthesis of penicillin, and the discovery of the most abundant photosynthetic organism on Earth are brilliant examples of how so-called ‘basic’ research has a direct connection with our society. Now, climate change has imposed new conditions and the future of organisms is uncertain; then plants, and especially bryophytes, could be a pivotal piece in understanding the effects of the coming challenges, and why not, part of the solution.

An announcement was published in the journal *Conversation* in London (July 2022), and they announced that "botanists are disappearing - just when the world needs them the most". While it's true that the training in this field is declining globally, the interest in knowing how plants survive, grow, and evolve still persists. Now - that I'll finish my dissertation in a few days - my focus is to show and educate new generations about the biology of plants, inviting students at an early age. I strongly believe that we need to make additional efforts for our children in the way we raise them, which most of the time is totally disconnected from nature. We, as educators, can contribute to introducing the natural world by showing them how fascinating, diverse, and dynamic the flora is around us. In this sense, bryophytes usually escape from the eyes of a nature-oriented excursion. However, as soon as people have first contact with them, they are usually fascinated by their biology, small size, and physiology. From the side of bryology, reviving botany is possible by showing how these little, tiny plants have big implications for our planet.

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Chapter 1

Patterns of diversity and community structure of mosses along an elevational gradient in Central Chile

Abstract

In the context of global climatic change, it is crucial to understand the spatial patterns of biodiversity and its underlying ecological and evolutionary mechanisms, including neglected groups in the tree of life such as bryophytes. To understand diversity patterns, we used phylogenetic approaches to measure diversity and structure in moss communities from the mountains of Central Chile. We sampled 25 sites along an elevation gradient, and each site was subdivided into three subsites corresponding to a gradient in soil moisture. We found that species richness and phylogenetic diversity (PD) showed a hump-shaped pattern along the elevation gradient. However, these metrics followed different trends depending upon the soil moisture. High richness and PD was found at the drier sites at low elevations but in the wettest sites at high elevations. The phylogenetic structure demonstrated that environmental filtering is the main driver of community assembly at low and high elevations, presumably associated with the harsh climatic conditions, while interspecific competition may not play a large role in community assembly. Similarity in community composition was more sensitive to phylogenetic turnover than to species turnover, both along the elevation gradient and the soil moisture gradient. This study highlights the utility of using spatial phylogenetics to infer the community structure and diversity of mosses at local scales.

Keywords: *Phylogenetic diversity, phylogenetic turnover, species richness, community structure.*

Introduction

A more complete understanding of how biodiversity varies across space would improve strategies for conserving life on our planet, while also providing insights into how organisms respond to changing environments (Colwell et al., 2008). Biodiversity has traditionally been viewed as taxonomic richness alone (MacArthur and Wilson, 1967), but now is recognized to be multidimensional, including phylogenetic and functional dimensions (Devictor et al., 2010; Mishler et al., 2014, Jarzyna and Jetz, 2016). Biodiversity integrates not only taxonomic information but also evolutionary and ecological approaches (Garnier et al., 2016). The phylogenetic component incorporates the degree of relatedness between organisms (Pavoine and Bonsall, 2011), whereas the functional component includes the diversity of functions in relation to the environment (Villéger et al., 2008).

Understanding the direct connection between history, traits, and ecological processes is important to understand the spatial patterns of biodiversity as well as ecological relationships among organisms (e.g., why one set of species co-occur within communities while others don't) (Webb et al., 2002; Cadotte et al., 2011). The co-occurrence of taxa is often not a result of random processes. Closely related species sometimes tend to occur together in communities because of their similar tolerance to the abiotic environment, known as "phylogenetic clustering" (Cavender-Bares and Wilczek, 2003; Kraft et al., 2007). If the abiotic environment (e.g., nutrient limitation, temperature, moisture) favors a suite of evolutionarily conserved traits that are shared by closely related species, then their distribution can be affected by a process known as "habitat filtering" (Kraft et al., 2014). In contrast, if competition is the dominant process, and thus the coexistence of closely related species is selected against, a community would tend to be composed of distantly related species, known as "phylogenetic overdispersion" (Webb et al*.,* 2002, Cavender-Bares and Wilczek, 2003).

Several tools have been designed for revealing the phylogenetic patterns in community assembly in the context of ecology and evolutionary history. Phylogenetic diversity (PD) is the total length of all phylogenetic branches required to span a given set of taxa in a location (Faith, 1992) and is useful for quantifying diversity in an evolutionary context (Mishler et al., 2014). Phylobetadiversity is a measure of phylogenetic turnover among communities based on the number of shared branches (Graham and Fine, 2008) and it is useful for inferring differences at local or regional scales. Both metrics follow the basic principles of traditional species alpha and beta diversity, respectively, but they add an important evolutionary depth (Cadotte and Davies, 2016).

Most studies in land plants using phylogenetic approaches in community assembly are carried out in vascular plants; the bryophytes (*e.g.,* mosses, liverworts, and hornworts) have been largely overlooked. Bryophytes play an important role in terrestrial and freshwater ecosystems, ranging from desert to temperate rainforests. For instance, they make important contributions to soil development, including aspects of nutrient cycling (Turetsky, 2003), influencing seed germination of other plants (Whitehead et al., 2018), water retention (Proctor, 2000), and erosion prevention (Seitz et al., 2017). They are also members of a fragile, yet crucial community in dryland ecosystems, the soil biocrust (Bowker et al., 2018). Bryophytes have unique biology as compared to vascular plants. The most remarkable traits in relation to survival and reproduction are reliance on asexual propagules, poikilohydry, and desiccation tolerance (Mishler and Oliver, 2009). Mosses can equilibrate their water content with their surroundings in a couple of seconds

(*poikilohydry*). They satisfy their water needs by absorbing water over the entire plant surface (Proctor, 2011), and can hydrate with rain, dew, or fog. During dehydration, the tissue rapidly dries out to become metabolically inactive, recovery from which many lineages of mosses are well-adapted (Gao et al., 2017). Most people associate bryophytes with wet and cold habitats, however, they can be one of the most dominant plants in driest areas of the world, such as deserts, or inhabit high altitudes, e.g., in the Alps where their elevational extend exceeds that found in vascular plants (Theurillat et al., 2003).

The flora and fauna in mountain systems change in composition and richness along with their elevational extent over a relatively short spatial scale (Körner, 2007), primarily because altitude drives changes in the abiotic environment such as temperature, water availability, and soil properties (Theurillat et al., 2003). Mountains play a significant role in creating new niches for animals and plants, can serve as both environmental refugia for older lineages or for radiations of new lineages, and may act as corridors for migration (Antonelli et al., 2009; Luebert and Weigend, 2014). In particular, the Andes − comprising North, Central, and Southern units along the west side of South America − is a mountain system that is widely known for its high levels of plant diversification in recent geological times, since the mid-Miocene, following its recent uplift during the last 15-20 million years (Luebert and Weigend, 2014; Hoorn et al., 2010). Mountains such as the Andes host a unique regional biota (Rahbek, 2005) that is spatially and phylogenetically heterogeneous. This makes the Andes an excellent natural system to study patterns of diversity and community ecology in a phylogenetic framework over short spatial distances for less understood organisms such as mosses.

While descriptive studies have been made worldwide in subalpine ecosystems (Theurillat et al., 2003), especially in the Neotropics due to the presence of the exuberant cloud forest (Churchill, 2009), only a few studies in southern South America have included bryophytes, despite the presence of a distinct set of moss communities (Müller, 2009). Central Chile is characterized by a predominantly Mediterranean climate, a fragile ecosystem with high levels of endemic flora, and represents a hotspot of biodiversity for vascular plants (Myers et al., 2000). Therefore, the study of bryophytes in central Chile to understand how these small organisms coexist in local harsh environments remains a fertile research topic. In particular, the coexistence of mosses along an elevational gradient coupled with phylogenetic approaches has never been studied in the mountain ecosystems of the Mediterranean-climate part of Chile.

This study combined several phylogenetic methods to investigate alpha and beta diversity in relation to community structure to gain a better understanding of the mechanisms influencing moss diversity along an elevational gradient in Central Chile. The hypotheses addressed in this study were: (1) Assuming that physiological traits are phylogenetically conserved, then abiotic conditions have selected for the co-occurrence of closely related species at low and high elevations as well as drier sites due to habitat filtering in harsher environments (2) Alternatively, if the physical environment plays a lesser role in shaping the community at mid-elevations, we hypothesize that community assembly is driven by competitive interactions within communities there (resulting in phylogenetic overdispersion). (3) High phylo-turnover occurs among sites along the elevational gradient due to phylogenetic niche conservatism and/or dispersal limitation.

Methodology

Sampling — Field sampling was conducted mainly in Altos de Lircay, Region del Maule (VII), and Aguas de Ramon, Region Metropolitana (RM), Chile; one site was obtained in Valle del Elqui, Region de Coquimbo (IV) Chile (Fig. 1.1, A). Central Chile extends from 32 to 37° south latitude. This area has predominantly a Mediterranean climate, which is characterized by having an alternation of dry, hot summers, and cold, rainy winters (Amigo and Ramirez, 1998; Luebert and Pliscoff, 2017). The vegetation ranges from spiny matorral in the driest areas (*Trevoa quinquenervia, Colliguaja odorifera, Acacia caven, Baccharis paniculata, and Schinus polygama*) to a sclerophyllous forest (*Quillaja saponaria, Peumus boldus, Cryptocarya alba, Lithraea caustica, Schinus latifolia, and Kageneckia angustifolia, Lomatia hirsuta*) mixed with deciduous forest (*Nothofagus obliqua, N.glauca, N. alpina, N. antarctica, N. pumilio*), evergreen forest (*N. dombeyi*), and alpine trees (*N. antarctica, N. pumilio, and Austrocedrus chilensis*) in the southernmost areas of Central Chile (Luebert and Pliscoff, 2017).

Sites were selected every 100 to 200 m. along elevation from 600 to 2,700 m (Fig. 1.1, B). A total of 25 sites of 15x5 m^2 were chosen at different elevations, and three plots (5x5 m^2) were selected within each site (Fig. 1.1, C). Sites represented the typical dominant vegetation in each altitudinal zone and the plots within each site were chosen according to a distance from a water source to reflect a local environmental gradient. That gradient was based on soil moisture, ranging from wet (plot A), medium moisture (plot B), and dry (plot C) areas at each site. The soil moisture was measured using a regular soil moisture meter (%) TekcoPlus Ltd. Usually, the source of water (creek or stream) was continuously flowing through the year and no wider than 5m. Small quadrants of 100x100cm^2 with internal grids of 10x10cm^2 were used to quantify the abundance of each moss species. The presence and abundance of moss taxa inhabiting soil or small rocks (excluding boulders) were recorded in each plot. Species inhabiting a soil substrate but located on roots were included in this study, but true epiphytes were excluded. Locations below 600m were not chosen for this study due to the presence of human activity; sites were avoided as well in areas surrounded by roads, trails, infrastructure, or any type of anthropogenic or agricultural activity.

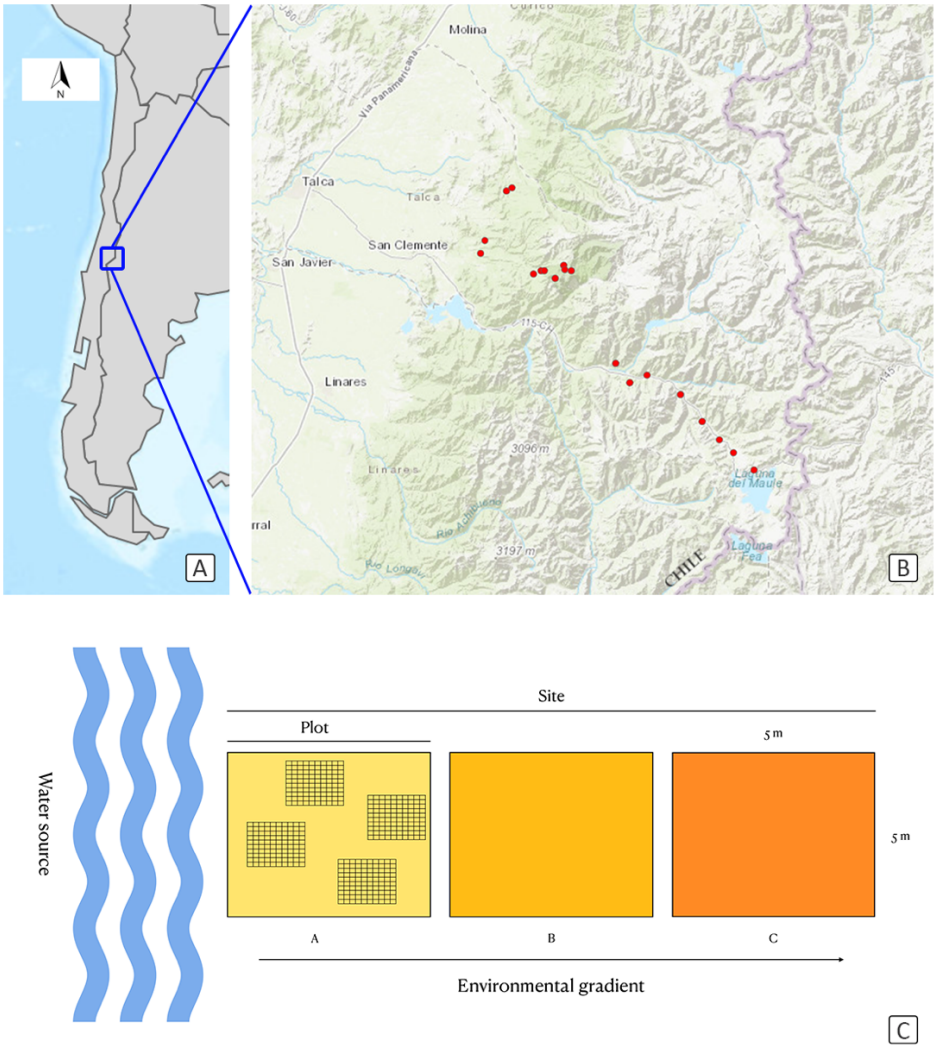

Figure 1.1. A: Map of Chile. B: Sampling points (red circles) of the sites along elevation in Region VII, Central Chile. C: Sampling design of sites and plots selected along elevation. Each site (15x5 m^2) was selected according to the presence of a water source (continuously flowing and < 5m of width) and dominant vegetation. We sampled three plots (5x5 m^2) within each site to create an environmental gradient according to the to the soil moisture. We measured the presence and abundance of terricolous and saxicolous mosses from four randomly sampled quadrants within a plot.

Species identification — We identified the species using regional taxonomic treatments of mosses in South America (e.g., *Didymodon*, Jimenez and Cano, 2006) or North America (*i.e.,* Bryacae, Spence, 2007) as well as local taxonomic treatments (Bartramiaceae, Matteri, 1985), and checklists of species from Chile (Müller, 2009). We also consulted with experts in certain taxonomic groups (personal communication with J. Brinda) or with specialists in moss taxonomy from Chile (personal communication with J. Larrain). In addition, we used Tropicos v3.3.2 (www.tropicos.org) and bryonames (www.bryonames.org) (Brinda and Atwood, 2021) to consult

and corroborate the nomenclature of names and classifications. All collected specimens were deposited in the University Herbarium at the University of California, Berkeley (UC).

Phylogenetic tree — We used well-known and widely available loci for phylogenetic inference in mosses: ITS (ITS2, 18s, and ITS5) as nuclear markers, and rps4, trnL-F and rbcL as plastid markers. The sequence data for each taxon and loci were obtained primarily from GENBANK; accession numbers are provided in Appendix A1. We created a supermatrix concatenating all loci. First, a blast search was used to find the sequences for each taxon. We merged two sequences in case of being identical or having complementary sequences to have a draft alignment for each locus in Aliview (Larsson, 2014). Subsequently, we concatenated the four alignments into a supermatrix using Aliview. Finally, we manually edited the concatenated alignment to resolve oddities in the alignment. Modelfinder was used to find the best model of evolution (Kalyaanamoorty et al., 2017) for each partition. We implemented each partition model to the concatenated alignment. In case a taxon was not available in GENBANK, we used a closely related species (see the OTU column in Appendix A1) to represent this specific taxon in the tree. All loci for *Syntrichia* species were obtained from a separate project in our lab that used a genome skimming approach. That dataset will soon be available (Mishler et al., in prep.). We inferred the phylogeny using a maximum likelihood (ML) approach implemented in IQ-TREE 2.1.3 (Nguyen et al., 2015).

Biodiversity measurements — We used Biodiverse v.3 (Laffan et al., 2010) to calculate Taxonomic Richness (TR), Phylogenetic Diversity (PD), Phylogenetic Endemism (PE), Shannon-Diversity Index (SI), and Relative Phylogenetic Diversity (RPD). We performed randomizations of the data using "rand structure" model to calculate randomized PD and RPD as calculated in Thornhill et al., (2016). The grid cell size was set to the size of individual plots (5x5 m^2).

Turnover — We used two clustering analyses, phylogenetic turnover (PhyloSorenson) and the traditional Sorenson index, to compare all plots to each other based on dissimilarity indices. Phylosorenson compares the dissimilarity between two labels (plots) in terms of branches of the phylogeny they share (Bryant et al., 2008), while Sorensen is a taxonomic approach that compares the dissimilarity between two plots, in terms of which taxa they share.

Results

Phylogenetic tree **—** The alignment consisted of 115 sequences with 1,644 parsimony-informative characters. The partition model suggested a model of evolution for each locus as follows: trnL-F: HKY+F+I; rps4: TVM+F+I; rbcL: GTR+F; ITS: TIM3+F+I. The best ML tree yielded a score of Lnl: -53779.2 (Fig. 1.2). The tree was rooted using *Spaghnum* and *Takakia*. The topology of the phylogenetic tree agreed with the most current phylogeny of mosses (Goffinet et al., 2009; Liu et al., 2019), except those members of Ditrichaceae (*e.g., Ditrichum*) were scattered among other clades in Dicranidae. We found well-resolved clades for different families of mosses as indicated in Fig. 1.2. Bryopsida was extensively represented by Dicranidae, Bryales, and Bartramiales. Hypnanae (pleurocarps) were represented by single lineages from scattered families of pleurocarps (Appendix A1).

Figure 1.2. Best tree (phylogram) from ML search performed in IQ-TREE 2.1.3. Bootstrap support for each node is indicated in black. Colored blocks indicate families, with blue indicating a large clade (*e.g.,* Bryaceae and Pottiaceae), purple mid-size clades (*e.g.,* Bartramiaceae and Grimmiaceae), and yellow small clades in terms of richness. Light blue indicated lineages represented by a single taxon.

Biodiversity measurements — We collected 417 bryophytes across all sites and these collections included 112 species. TR and SI followed a hump-shaped pattern along the elevation gradient from 600 to 2,700 m (Fig. 1.3), in which mid-elevation sites had the highest level of species richness and Shannon-diversity index, compared to the low or high elevation sites. The observed TR, PD, PE, and SI are shown in Fig. 1.3. As expected, TR and PD followed similar distribution values across all the sites and plots (Thornhill et al. 2016). The highest values of PD and TR are concentrated at mid-elevation sites, in which we found around 10 to 14 species. The highest values were found in plots next to the water source (plot A) or close to it (plot B). Similar to TR and SI, high PD was concentrated in most humid plots at high elevations, but farthest from the water source at low elevations. PE followed a similar trend to PD and TR, but also there were few high values distributed in high elevation sites, especially farthest from the water source.

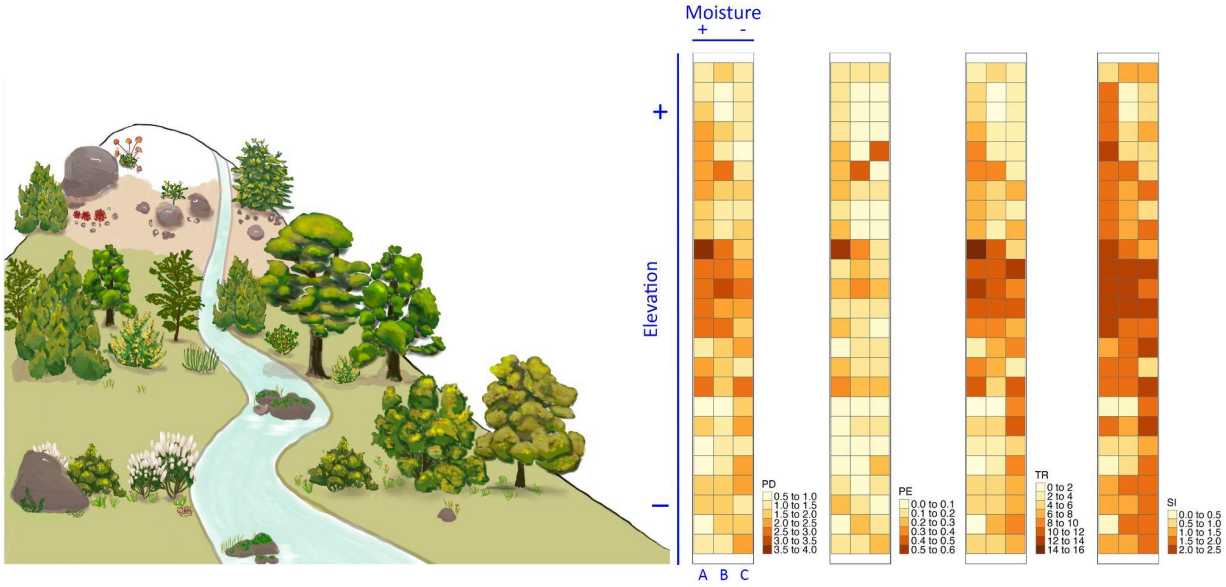

Figure 1.3. Biodiversity measurements (PD: Phylogenetic diversity; PE: Phylogenetic endemism; TR: Taxonomic richness, SI: Shannon-Diversity Index) along elevation.

Significant RPD and PD — Areas of significant PD and RPD showed contrasting patterns (Fig. 1.4). For PD, significant areas of low PD were found at low and high elevations, indicating phylogenetic clustering in those plots. A few plots of low PD were found at mid-elevation, especially in the driest plots. Only one plot showed high PD, indicating phylogenetic overdispersion. Significantly high RPD was mostly found from mid to high elevation, indicating significant longer branches than expected by chance. Only a few plots with significantly low RPD were found at mid-elevation at the driest plots indicating significantly shorter branches than expected by chance.

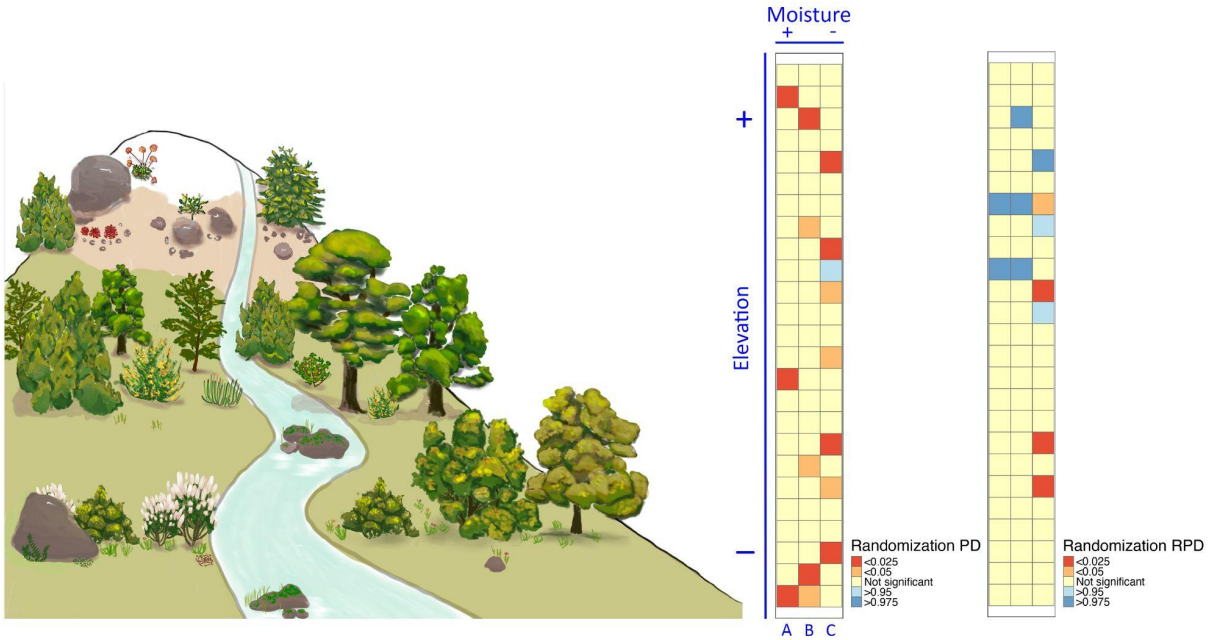

Figure 1.4. Biodiversity measurements (Randomization of phylogenetic diversity; Randomization of relative phylogenetic diversity) along elevation.

***Turnover* —** Phylosorensen and Sorensen analyses suggested several major clusters (Fig. 1.5). Phylosorensen clusters reflected more closely the changes in elevation and distance from the water source than did Sorensen. For Phylosorensen, there were two large clusters (red and green in Fig. 1.5, A) that reflected the changes in moss communities according to soil moisture (plot A and B vs plot C). Clusters shown in purple, orange, and yellow in Fig. 1.5, A, were associated with the turnover of communities according to elevation. In contrast, Sorensen mostly reflected the soil moisture gradient (Fig. 1.5, B). Of the two largest clusters, the red cluster was associated with plots closer to the water source (plot A), while the blue cluster in Fig 1.5, B, linked drier areas (plots B and C) independently of elevation.

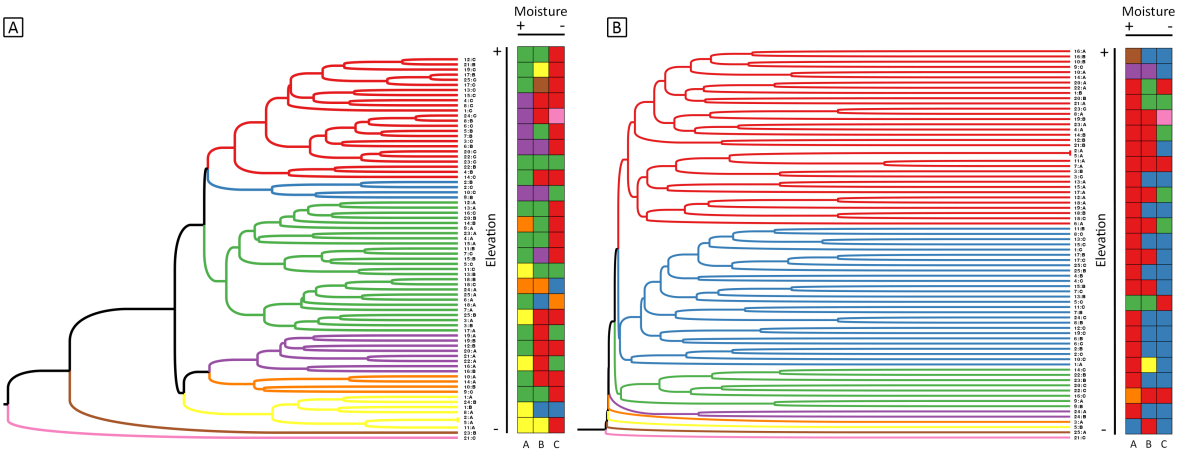

Figure 1.5. Dendogram and grid cells along elevation showing the degree of similarity of the moss communities based on shared branches across the phylogeny (Phylosorensen) (A) and shared terminals across the phylogeny (Sorensen) (B). Phylosorensen discriminated clusters associated with changes in elevation and soil moisture (red and green colors), while Sorensen suggested changes across the soil moisture (red and blue colors).

Discussion

The pattern of taxonomic richness and abundance in response to elevation in mountainous regions of Central Chile follows a humped-shaped pattern (Fig. 1.3). Although there are three well-established patterns of richness (in vertebrates and vascular plants) along elevational gradients (monotonically decreasing richness at higher elevations, a low-elevation plateau with a mid-peak, and humped-shaped patterns; Rahbek, 2005), studies of bryophyte richness along elevation gradients are few, and previous studies have found no consistent pattern. These studies have reported decreasing richness with increasing elevation (Tussime et al., 2007), increasing richness with increasing elevation (Frahm and Ohlemüler, 2001, Bruun et al., 2006), a hump-shaped distribution (Grau et al., 2007; Sun et al., 2013, Ah-Peng et al., 2014), or no clear trend in richness with elevation (Grytnes et al., 2006). A consensus among bryophyte studies suggests the pattern is taxon-specific, highly linked to the ecology or evolutionary history of particular clades, and single/multiple causes can be responsible for the observed pattern (Lomolino, 2001; Körner, 2007; McCain and Grytnes, 2010).

In this study, taxonomic richness and Shannon diversity depended on the soil moisture gradient (distance from a water source) but followed contrasting trends as elevation increased. Richness and Shannon diversity were higher in most humid plots (plot A, closer to the water source) at high elevations, but higher in the driest plots (plot C, farthest from the water source) at low elevation (Fig. 1.3). Besides the increasing species richness on those sites, there was an increasing uniformity of the distribution of individuals among the species. Thus, while soil moisture is an important microenvironmental condition, its influence on species richness depends

on elevation in mountainous regions of Central Chile. It is traditionally thought that vascular plants' distribution along elevational gradients are governed by temperature-related processes and gradual changes in the physical environment (Grytnes et al., 2006; Kreft and Jetz, 2007); however, bryophytes are less influenced by macroclimatic temperature or precipitation and more influenced by the presence of microenvironments (Hedderson and Brassard, 1990; Theurillat et al., 2003; Patiño and Vanderpoorten, 2018). In bryophytes, factors operating at smaller scales have gained more attention (Grytnes et al. 2006) given their small size and poikilohydric water relationships. For example, the highest richness along an elevation gradient coincides with greater diversity and quality of substrate (*e.g.,* pH), but less with macroclimatic conditions (*e.g.,* annual precipitation or temperature) (Pharo and Beattie, 2002; Sun et al., 2013). In Chile, the peak abundance of epiphytic bryophytes has been attributed to high humidity in form of mist, dew, or clouds, at low to mid-elevation in the coastal mountain range (Frahm, 2002).

The pattern of richness mirrored that of phylogenetic diversity and endemism. It is known that species richness is correlated with phylogenetic diversity; in fact, that is the null expectation if species are associated randomly with respect to phylogeny (Thornhill et al., 2016). In our study, high levels of phylogenetic diversity were found at mid-elevation sites at any level of soil moisture. For example, high PD, PE, and TR were found in a plot that contained 15 species that comprised a great part of the phylogeny (Fig. 1.3). Likewise, high phylogenetic diversity was associated with the moist humid plots at high elevation, and with the driest plots at low elevation. High phylogenetic endemism was found at mid to high elevations, reflecting the range-restriction of the branches occurring in those plots. For example, *Andreaeae* had long branches restricted to high elevations. *Schistidium andinum, Hennediella kunkzeana, Weissia controversa* were some of the species were restricted to areas of mid-high elevation.

However, we found many non-random patterns of phylogenetic structure in our study. The randomization test of PD revealed some possible influences of ecological processes on the observed pattern of diversity. Assuming that physiological traits are phylogenetically conserved, habitat filtering can lead to the coexistence of closely related species (phylogenetic clustering). We found significant phylogenetic clustering in several plots at low and high elevations (Fig. 1.4). On the other hand, if interspecific competition is the dominant ecological force, then communities would tend to contain distantly related species (phylogenetic overdispersion). Although we observed high phylogenetic diversity at mid-elevation, there was only one plot showing significantly high PD (i.e., phylogenetic overdispersion). Thus, competition appears not to be a major driver of community assembly in this system. Studies in angiosperms have also shown phylogenetic clustering at high and low elevations in Changbaishan (Qian et al., 2014) and Mount Tai (Zhang et al., 2016), China. Similar phylogenetic community structure patterns have been reported for distantly related organisms, such as butterflies (Pellissier et al., 2013) and ants (Machac et al., 2011) along elevation gradients.

As inferred from PD and RPD, the results of this study suggest that environmental filtering is one of the main drivers of moss community assembly at high and low elevations in mountainous regions of Central Chile. High elevation sites tend to have lower temperatures and are covered by snow during winter and spring; while low elevation sites tend to be dry and hot during spring and summer (influenced by the dominant Mediterranean climate). Lineages occurring at low and high elevations have likely evolved the ability to tolerate such harsh conditions. Indeed, the most dominant families are Bryaceae (Gao et al., 2017) and Pottiaceae (Cevallos et al., 2019), which have many species known to be desiccation-tolerant. Indeed, some lineages of mosses inhabiting dry conditions are able to absorb water from dew and externally transport and store water for a

long period of time to perform photosynthesis (Proctor, 2011). Functional trait-based approaches suggest that the dominance of cushions or erect turf growth form or the presence of traits such as cell ornamentation, excurrent nerves, and leaf margin recurvature (Henriques et al., 2017) might be associated with high water-holding capacities by limiting evaporation (small surface to volume ratio) (Zotz et al., 2000). Ah-Peng et al., (2014) and Souza et al., (2020), showed that water-related traits in mosses changed markedly over time and along environmental gradients presumably associated with increasing harshness.

Despite the lack of PD-significance among the mid-elevation sites, they did present high raw phylogenetic diversity. High phylogenetic diversity, like high richness and Shannon diversity, suggests higher heterogeneity of habitats. Mid-elevation sites offered a suite of opportunities for establishment, survival, growth, and reproduction across different lineages since there are dominant *Nothofagus* forest mixed with matorral sclerophyllous forest. The dense foliage of *Nothofagus* creates different microenvironmental under their canopy, including low light penetration, high moisture, and lower temperature than open spaces (Frahm, 2002). Microhabitats occur among the roots at the base of vascular plants or between rocks on soil, where organic matter accumulates. The accumulation of organic matter, along with low disturbance, provides a substrate with extraordinary moisture-holding capacities that can be exceedingly beneficial for several lineages of mosses (Sun et al., 2013). The mixed forest provides more resources and ecological niches for a diverse set of moss lineages at mid-elevation, in the ecotone between *Nothofagus* forest and montane ecosystems (Elias et al., 2016).

Part of the explanation for the phylogenetically random community assembly found at mid-elevations might be a result of facilitation rather than competition or environmental filtering. Facilitation has been neglected in ecological studies, which often overemphasize negative biotic interactions (predation or competition) (During and Van Tooren, 1990). Positive interactions could play an important role in the community assembly of mosses increasing diversity due to the differing regeneration niches of distant lineages (Valiente-Banuet and Verdú, 2013). Indeed, this pattern has been studied previously in several alpine environments, including the Andes of Chile (Anthelme et al., 2014; Valiente-Banuet and Verdú, 2007). Many bryophytes tend to occur in aggregated cushions, which allows for better water-holding capacities and photosynthesis as compared to isolated plants (Cornelissen et al., 2007). These positive interactions of high-density-dependent systems might be typical for poikilohydric organisms (During and Van Tooren, 1990). Conservation plans should consider this information to preserve areas of high taxon richness and high phylogenetic diversity.

The plots were more structured in their patterns of similarity along the elevation gradient and across the soil moisture gradient when measured with phylogenetic turnover, as compared to species turnover metric (Fig. 1.5, A). This reflects the importance of incorporating shared branches of the tree (phylogenetic signal) rather than just species similarity. The largest clusters (shown in green and red in Fig. 1.5) were communities of mosses that shared lineages well-adapted to either high moisture (plot A: *Bartramia, Vittia,* and *Pohlia*) or dry conditions (plot B or C: *Didymodon, Hennediella,* and *Syntrichia*). The purple cluster in Fig. 1.5 contained communities at high elevations that comprises long and short branches (*e.g., Vittia, Bryum, Pohlia, Cratoneuropsis,* or *Philonotis*), while the yellow cluster contained small communities in terms of species with short branches at low elevation (*e.g., Hymenodontopsis*). One of the smallest clusters (pink in Fig. 1.5) contained two long branches of species of *Andreaea* that inhabited small rocks on drier areas at high elevation. These examples highlight the result that habitat type along the moisture gradient and elevation drives changes in the phylo-turnover metric.

On the other hand, taxonomic species turnover found stronger differences across the soil moisture gradient compared to elevation (Fig. 1.5, B). Species living closer to the water source were widely distributed along the elevation gradient. For instance, *Vittia pachyloma* and *Bartramia ithyphylloides* were two species widely distributed in plots closer to the water source independently of elevation. Likewise, *Syntrichia* species were distributed in the driest plot along the elevation extent.

In general, species with greater dispersal abilities might reach new areas more easily. Comparing species turnover among spermatophytes, pteridophytes, and bryophytes, studies have found that the two latter groups, whose propagulae are spores, have lower turnover rates than spermatophytes because of their lower distance-decay rates (decreasing similarity with increasing distance between sites) (Nekola and White, 1999; Qian, 2009). Our results aligned with this observation. For instance, species from plots B or C in mid-elevation might easily be dispersed to higher or lower plots to establish in the same habitat types, while aquatic mosses might use the water source to disperse plant fragments and establish on another aquatic substrate. We suggest dispersal capabilities of mosses lead to lower species and phylo-turnover across elevation and thus more similar communities within each plot. Further studies should consider the importance of dispersal ability/limitation in small organisms in shaping communities.

Methodological concerns are commonly reported in the literature when estimating species diversity along an elevational gradient (Rahbek, 2005; McCain and Grytnes, 2010). This study might contain some of the reported biases in its observed patterns of diversity. The scale, sampling, and anthropogenic activity (Cavender-Bares et al., 2009; Gotelli and Cowell, 2011; Geffert et al., 2013; Chen et al., 2015) are potential factors that might influence our results. This short-term study might have missed rare species or under-sampled some plots. For instance, high elevation sites were covered by snow most of the time, leaving a limited window of time or a restricted area for sampling. In addition, there were some anthropogenic disturbances, such as camping, bushwalking, and cattle, that created fragmentation of the landscape at low elevations.

Nonetheless, the results presented here include a community of bryophytes and local microclimatic conditions that are broadly representative of Central Chile. The phylogenetic structure found in this study can provide useful insight into community assembly, a foundation for testing ecological theories on community assembly, and a basis for the understanding of ecosystem functioning on a global scale. Given the unique biology of bryophytes (e.g., desiccation tolerance and poikilohydric) and enormous contribution to ecological functions, further studies should be undertaken, in conjunction with functional diversity and local measurements of microenvironmental conditions, to gain a deeper understanding of the mechanisms driving diversity in less well-studied groups such as mosses.

Chapter 2

The phylogeny of *Syntrichia* Brid.: An ecologically diverse clade of mosses with an origin in South America

Abstract

Premise of the study: To address the biodiversity crisis, it is important to understand the evolution of all organisms and how they fill geographic and ecological space. *Syntrichia* is one of the most diverse and dominant genera of mosses, ranging from arctic-alpine habitats to desert biocrusts, yet its evolutionary history, trait evolution, and origins are still unclear.
Methods: We present a comprehensive phylogenetic analysis of *Syntrichia,* based on both molecular and morphological data*,* with most of the named species and closest outgroups represented. In addition, we provide ancestral state reconstructions and a global biogeographic analysis.
Key results: Syntrichia is a clade that includes several previously accepted genera. We found 10 major well-resolved subclades with geographical or morphological coherence. *Syntrichia* originated in the southernmost part of South America in the early Eocene (56.5–43.8 mya), subsequently expanded its distribution to the Neotropics, and finally dispersed to the Northern Hemisphere. There, the clade experienced recent diversification (15–12 mya) into a broad set of ecological niches (e.g., the *S. caninervis* and *S. ruralis* complexes). The transition from terricolous to either saxicolous or epiphytic habitats occurred more than once, and this is associated with changes in water-related traits.
Conclusions: Our results provide a framework for understanding the evolutionary history of *Syntrichia* through the integration of morphological and molecular characters. These findings highlight the likely biogeographic processes shaping the current distribution of the clade, with implications for morphological character evolution in relation to niche diversity.

Keywords: Syntrichia, biogeography, systematics, long-distance dispersal, water-related traits, South America.

Introduction

In the midst of the current biodiversity crisis, it is imperative to better understand diversity in the many underexplored clades in the tree of life. Most studies on plant biodiversity have focused on vascular plants and the bryophytes have been relatively overlooked (Shaw and Renzaglia, 2004). This glaring omission is alarming, especially in light of their global species diversity (around 20,000 to 23,000 named species; Crum, 2001; Brinda and Atwood, 2021), which far exceeds that of many groups of vascular plants such as ferns (~13,000 sp.; Hassler, 2004) or gymnosperms (~1,100 sp.; Forest et al., 2018). Phylogenetic provide in-depth knowledge of how underlying biological processes have generated patterns of diversity (Helmus et al., 2007; Smith et al., 2020). A phylogenetic tree is a basis for organizing and retrieving all our knowledge about biodiversity (Soltis and Soltis, 2003). Thus, it is crucial to include phylogenetic analyses of lesser-studied organisms, in the appropriate spatial context, to better understand the processes of ecology and evolution (Thornhill et al., 2016, 2017).

Bryophytes play significant roles in ecosystem functioning, such as nutrient cycling (Turetsky, 2003), water retention (Proctor, 1982; Proctor, 2000), and preventing soil erosion (Seitz et al., 2017). Bryophytes tend to be small plants and so are often unfairly characterized as 'simple' or 'primitive' regarding their structure and physiology (Mishler and Oliver, 2009). Nevertheless, they are wildly abundant in tropical forests and humid temperate forests (Geffert et al., 2013) and are essential elements of the flora in harsh environments (Zander, 1993), such as in deserts (Vanderpoorten and Goffinet, 2009), where they are a living part of the soil (the biotic soil crust) in association with lichens and cyanobacteria (Bowker et al., 2018). As dominant members of various cryptogamic communities, *Syntrichia* species can also significantly influence ecosystem function. For instance, *S. caninervis* and *S. ruralis* are major contributors to the formation of biocrust communities, while several other species often dominate moss communities on trees (e.g., *S. latifolia*, *S. papillosa,* and *S. pagorum*).

Bryophytes often have a wider distribution than vascular plants, particularly when comparing higher taxonomic levels (Tan and Pócs, 2000). This may be partly due to different ranking criteria applied to bryophytes as compared to vascular plants. Yet their small size, abundance of resilient spores, and diversity of asexual propagules enable bryophytes to disperse across the landscape efficiently (Medina et al., 2011). Bryophytes have been subjected to the same evolutionary forces through time and space, and their large-scale biogeographic patterns are largely congruent with those reported in other groups of plants (Patiño and Vanderpoorten, 2018). Vicariance and more recent long-distance dispersal (LDD) are the two main explanations given for the distribution of vascular plants. With new advances in phylogeny reconstruction and estimation of divergence times, LDD has become the main mechanism to explain disjunct distributions in vascular plants (de Queiroz 2005) and in bryophytes (Patiño and Vanderpoorten, 2018). For example, in some lineages of liverworts (Bechteler et al., 2017) or mosses (Shaw et al., 2003), the current distributions are primarily explained by dispersal. This confirms that bryophytes are dynamic with respect to their distribution yet are affected by a variety of different biogeographic processes. Despite numerous hypotheses suggesting that diaspores are sometimes borne on air currents or carried by migratory birds to disperse to new regions (Gillespie et al., 2012; Lewis et al., 2014; Lewis et al., 2017), bryophytes likely move mostly by slow expansion, perhaps using shorter distance dispersal along island or mountain stepping stones (Medina et al.,

2011). Sorting out the relative contribution of different causes of the biogeography of mosses remains an open question, and phylogenies are an important tool for its resolution.

Syntrichia Brid. is one of the most diverse and complex genera of Pottiaceae, a family of mosses characteristic of harsh environments (Zander, 1993). It contains 87 currently accepted species-rank taxa (Brinda and Atwood, 2021) and is distributed worldwide in nearly all terrestrial ecosystems. About 40–50% of the species occur in the Neotropics (Churchill et al., 1995; Churchill, 2009), mostly from the tropical Andes, or temperate forests in the southernmost ecoregions of South America (Ochyra et al., 2008; Müller, 2009). Its widespread and diverse nature makes *Syntrichia* an excellent biogeographic study system. Although the distribution of *Syntrichia* as a whole is cosmopolitan (Zander, 1993), it contains several apparent disjunctions across continents, including between the Northern and Southern Hemispheres (Mishler, 2007), as well as taxa with quite small distributions (Gallego and Cano, 2009; Gallego and Cano, 2021). Several taxa are considered uncommon, rare, or endemic (Gallego et al., 2014, Gallego et al., 2020). The processes causing these disjunct distributions are likely much more recent than explanations involving continental drift; however, calibrated phylogenies and biogeographic analysis, which includes different biogeographic models, can help reveal the biogeographic history of *Syntrichia*.

In terms of morphology, *Syntrichia* presents a striking disparity of characters that is not observed in related groups (i.e., *Tortula* or *Hennediella*), especially in leaf shape, leaf ornamentation, and costa anatomy (Fig. 2.1). Stem size ranges from massive (12 cm) to relatively small (0.1 cm). Leaf shape ranges from strongly lanceolate with prominent teeth at the margin, to spatulate with an entire margin. Some species have strong, serrate hairpoints that sometimes double the length of the leaf, while others have a complete absence of hairpoints (see Gallego and Cano, 2009). However, shared characters among all species are a red reaction to KOH, a cross-section with a dorsal stereid band, and an abruptly differentiated group of hyaline basal cells (Mishler 2007). Much of this disparity of morphology might be related to differing water relationships in the various habitats where the species occur. Mosses appear to have evolved different adaptations to water uptake and movement than vascular plants due to being poikilohydric (Hébant, 1977; Ligrone et al., 2012) and desiccation-tolerant (Proctor et al., 2007). This plesiomorphic trait of poikilohydry (shared with the aquatic algal ancestors of land plants) allows mosses to respond directly to water in their surroundings including dew or fog (Proctor, 2000). Most mosses rely on external water conduction for survival and reproduction (Proctor, 1979; Proctor and Tuba, 2002), and *Syntrichia* relies on external water transport and absorption over the entire plant surface (Proctor, 1979). Given the disparity of morphological characters and the wide range of physiological performance in *Syntrichia*, it is likely that some characters are associated with the environment (Coe et al., 2019). Thus, understanding the evolutionary history of the extant species will help our understanding of how and when these distinctive characters arose. A phylogenetic framework is required to address the association of ecology and the function of the character of interest over evolutionary time (Mishler, 1988).

Despite its remarkable morphological diversity and cosmopolitan distribution, *Syntrichia* is thought to be monophyletic (Mishler, 2007) and distinct from the closely related genus *Tortula* (Zander, 1993). Since Zander's circumscription, *Syntrichia* has been adequately defined and more and less stable taxonomically, although recent publications have transferred some species from one genus to another (Gallego et al., 2011; Gallego et al., 2014; Brinda et al., 2021), synonymized some taxa (Gallego et al., 2009, 2011), or described new species (Gallego et al., 2020; Gallego and Cano, 2021). For example, Gallego (2005) proposed a taxonomic treatment for the species

from the Mediterranean region and Macaronesia, multiple new species from South America have been described (Gallego et al., 2020; Gallego and Cano, 2021), and Mishler (2007) provided a comprehensive treatment for North America.

Despite the importance of generating regional taxonomic treatments of *Syntrichia*, only a few phylogenetic analyses have been performed, and these have only focused on a particular subclade (Gallego et al., 2014) or geographic area (Hedenäs et al., 2019), relatively few, distantly related taxa (Spagnuolo et al., 1999), or a restricted number of molecular markers (Mishler et al., in prep). The integration of morphological characters with molecular data for phylogeny reconstruction has been done in angiosperms (Nickrent, 2019), gymnosperms (Escapa and Catalano, 2013), and ferns (Rothwell and Nixon, 2006), but rarely in bryophytes. One of the main reasons is the scarcity of appropriate methodological approaches for incorporating multistate morphological characters along with matrices of molecular data. There has been an explosion of available molecular data for phylogenetics, which some might argue swamps out any role for morphological data (Lee and Palci, 2015). However, we believe that mosses have many well-defined, independent morphological characters suitable for phylogenetic analysis. In particular, *Syntrichia* presents an abundance of gametophytic and sporophytic characters, a variety of characters rarely seen in other taxa in Pottiaceae. We feel that the morphological data need to be integrated with the molecular data for many purposes in phylogenetics (Mishler, 2005, 2014).

In this study, we present a robust global phylogeny of *Syntrichia* inferred from a large dataset that integrates molecular and morphological data. The goals of this study were to: (1) reconstruct the phylogeny of *Syntrichia* using a target enrichment approach for DNA sequence data plus rigorous scoring of morphological characters, (2) reconstruct ancestral states for ecologically related traits, and (3) perform a biogeographic analysis. Our hypotheses associated with these goals were: (1) *Syntrichia* is monophyletic group with geographically defined internal nodes, (2) soil substrate is the most likely ancestral condition for *Syntrichia*, which later diversified into other habitats, and (3) the genus had a southern South American origin, with subsequent dispersal events to the Northern Hemisphere using the Andes and mountains in Central America as the main stepping stones to North America.

Figure 2.1. Leaf variation in *Syntrichia*, emphasizing leaf shape and specialized cells in the costa. A: Leaf shape and costa x.s. of *S. princeps*, *Brinda 8400*; B: Leaf shape and costa x.s. of *S. pseudorobusta*, *Ireland 35943*; C: Leaf shape and costa x.s. of *S. breviseta, Larraín 40500*; D: Leaf shape and costa x.s. of *S. robusta, Brinda 5305*. E: Leaf shape and costa x.s. of *S. saxicola, Larraín 33119*; and F: Leaf shape and costa x.s. of *S. ruralis, Brinda 9108*.

Methodology

Taxon sampling **—** A total of 98 accessions were used for the phylogenetic analysis, representing most of the named species of *Syntrichia* worldwide (the missing species are distributed mostly in South America). We also included 19 accessions representing close relatives of *Syntrichia*, including *Barbula unguiculata* Hedw., *Chenia leptophylla* (Müll. Hal.), *Dolotortula mniifolia* (Sull.) R.H. Zander*, Hennediella antarctica* (Ångstr.) Ochyra & Matteri, *Hennediella stanfordensis* (Steere) Blockeel*, Leptodontium capituligerum* Müll. Hal*., Leptodontium pungens* (Mitt.) Kindb*., Sagenotortula quitoensis* (Taylor) R.H. Zander*, Saitobryum lorentzii* (Müll. Hal.) Ochyra*, Streblotrichum convolutum* (Hedw.) P. Beauv*., Streptopogon erythrodontus* (Taylor) Wilson ex Mitt*., Tortula inermis* (Brid.) Mont*., Tortula muralis* Hedw*., Tortula plinthobia* (Sull. & Lesq.)*, Tortula subulata* Hedw., *Trichostomum brachydontium* Bruch, *Willia austroleucophaea* (Besch.) Broth*.,* and *Willia brachychaete* (Dusén) R.H. Zander.

Each named species was represented by one accession that was carefully examined for correct identification. Microscopic examinations were carried out guided by keys for the genus (Kramer, 1988; Zander, 1993; Mishler, 1994, 2007; Ochyra et al., 2008; Gallego and Cano, 2009) using a dissecting and compound microscope (Leica model MZ6 and Leica model laborlux S).

To address questions about the historical biogeography of *Syntrichia* and its closest relatives, we also included four more distantly related taxa to calibrate the phylogeny: *Ceratodon purpureus* (Hedw.) Brid*., Leucobryum glaucum* (Hedw.) Ångstr*., Cynodontium tenellum* (Schimp.) Limpr*.,* and *Rhabdoweisia fugax* (Hedw.) Bruch & Schimp. We used the permineralized fossil *Cynodontium luthii* Bippus, G.W. Rothwell & Stockey, discovered in Alaska (Bippus et al., 2021), to estimate the minimum age of Rhabdoweisiaceae and to calibrate the phylogeny.

We were able to represent most of the Old World and New World species of *Syntrichia* using herbarium specimens. A few specimens were fresh collections by the first author. Voucher specimens for these field collections were deposited in the University Herbarium, University of California, Berkeley (UC). The herbarium specimens used (with permission) for sequencing were from UC, California Academy of Sciences (CAS), and Missouri Botanical Garden (MO). All specimens are listed in Appendix B1 (see Supplemental Data with this article). We sampled a single genotype (one stem from each clump), leaving the remaining tissue in a separate small packet within the larger voucher packet.

Molecular dataset **—** The molecular dataset was obtained using targeted enrichment sequencing working with the Genealogy of Flagellate plants project (GoFlag). We used the GoFlag 408 flagellate plant probe set, which targets 408 relatively conserved exons from single or low copy nuclear genes (Breinholt et al., 2021). The DNA was extracted using the cetyltrimethylammonium bromide (CTAB) protocol as described by Doyle and Doyle (1987) with slight modifications described in Breinholt et al. (2021). The library construction, target enrichment, and sequencing were performed by RAPiD Genomics (Gainesville, Florida, USA) following protocols described in Breinholt et al. (2021). We used the six-step pipeline (trim reads, assembly, probe trimming, orthology to reference, contamination filter, multiple sequence alignment, and merge isoforms) detailed in Breinholt et al. (2021) to assemble alignments of the target regions from the raw sequence data. In some cases, this pipeline will result in multiple sequences from a single sample for a locus, which could represent paralogs. In order to minimize the possible effects of paralogy in our analyses, if the alignment for any locus included multiple

sequences from a sample, we removed all sequences from that sample from the locus alignment, thus retaining only samples represented by a single sequence. We also trimmed the sequence alignments by removing any columns with fewer than ten nucleotides using a custom Perl script. The raw sequence data used in this study will be available in the NCBI SRA database through BioProject PRJNA853349 (see Appendix B1 for accessions).

Morphological dataset **—** We created a morphological matrix using Mesquite v 3.7 (Maddison and Maddison, 2021) that included 43 characters (both gametophyte and sporophyte traits) in total for the 98 accessions (the main characters are illustrated in Fig. 2.2, while a detailed description of characters and their states are listed in Appendix B2). Permanent microscopic slides were also made from each specimen. The characters were scored using the same specimen we used as the source for molecular data. We scored missing data as (-), and if the specimen didn't provide enough information to describe gametophytic or sporophytic characters, we consulted regional and local taxonomic treatment literature for the taxon in question (e.g., Mishler, 1985).

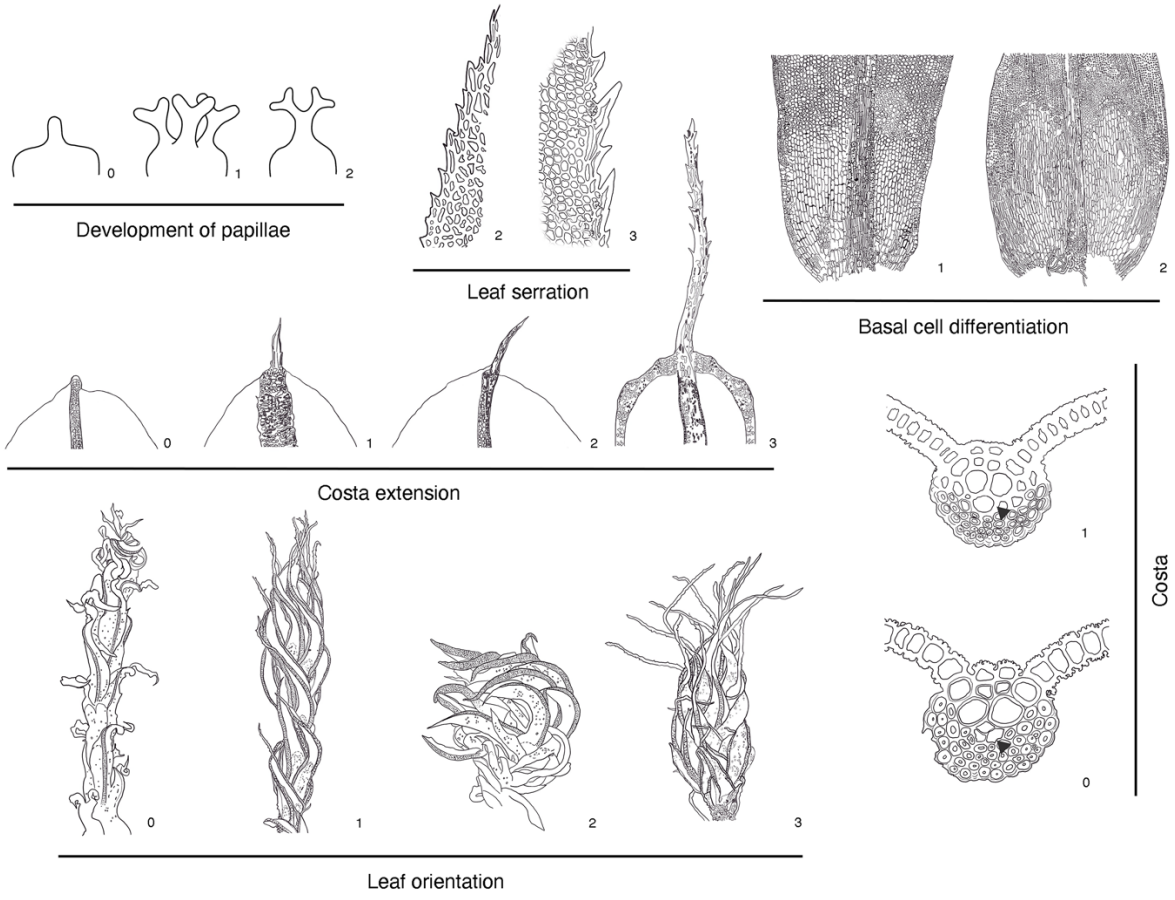

Figure 2.2. Morphological characters and states in *Syntrichia*. Development of papillae: a projection from cell surface developed by successive bifurcations. 0= simple; 1= standard branching; 2= antleroid branches. Leaf serration: Projections in the form of teeth in the margin. 0= entire*; 1= irregularly toothed near apex*; 2= short (unicellular) in lamina; 3= long (multicellular) along the margin below the apex. Leaf orientation (dry): arrangement of leaves around the stem. 0= leaves individually crisped (strongly wavy); 1= leaves individually twisted (bread); 2= leaves twisted together around stem, longitudinally infolded (rosette or bulbiform); 3= appressed or imbricate (e.g., *S. caninervis*);

4= leaves in rosette but crisped*. Costa extension: 0 = costa percurrent (present throughout the leaf, but not extending beyond lamina); 1= costa excurrent as mucro; 2 = costa excurrent as short awn (spine); 3 = costa excurrent as a hairpoint. Subguide cells: Presence of cells with large lumens abaxial to guide cells. 0 = absent; 1 = presence. Hydroids: Any recognizable differentiation of hydroids. 0 = present; 1 = absent. *: Morphological states that are not illustrated in the figure.

Phylogenetic analysis **—**Tree inference was performed using IQ-TREE 2.1.3. (Nguyen et al., 2015), and the morphological data were included with the molecular matrix using a partition analysis with mixed data. We implemented a Mk+ASC Model for the morphological data, while we used a GTR+G+I model for the molecular dataset. The ultrafast bootstrap (UFBoot) analysis was performed to assess the robustness of the ML tree (10,000 replicates; Hoang et al., 2018). We also performed tree inference using the morphological and molecular datasets by themselves for comparison with the tree inferred from the combined dataset.

Calibration **—** We implemented a strict molecular clock using a Bayesian approach available in BEAST v2.6.6 (Bouckaert et al., 2014). A node-dating approach was implemented to calibrate this ultrametric tree using a single fossil (*Cynodontium luthii*, Rhabdoweisiaceae; Bippus et al., 2021) found on the North Slope of Alaska from the Late Cretaceous. Therefore, the minimum age of the clade Rhabdoweisiaceae was bracketed between 66 and 84 mya (Santonian to Maastrichtian age). A uniform probability density as prior for the calibrated node was used for calibration of the phylogeny (Heath, 2012). The root, calibration point, probability density, nucleotide substitution model (GTR+G+I), and tree topology (derived from the integrated dataset) were used as priors for the analyses. A birth-death model was used for estimating the divergence time. Two independent Markov Chain Monte Carlo (MCMC) runs were conducted for 10,000,000 generations. The initial 20% of the trees were removed as burn-in. Tree annotator (as part of BEAST package) was used to summarize a sample of trees from BEAST and to annotate posterior probabilities and HPD node heights. The trees were visualized in the software application FigTree v1.4.4.

Biogeographic analysis **—** Six biogeographic areas of the world were used for the biogeographic analysis, delimited using tectonic plates: (A) South America, (B) North America, (C) Eurasia, (D) Africa, (E) Australia, and (F) Antarctica. We used BioGeoBEARS implemented in R (Matzke 2013a) to infer the biogeographic history of the taxa via probabilistic modeling of geographic range evolution. We compared the DEC, DEC+J, DIVAlike, DIVAlike+j, BAYAREAlike, and BAYAREAlike+j models to test the significance of each model in the same dataset (Matzke, 2014). The distance-extinction-cladogenesis (DEC) was designed by Ree and Smith (2008) to test the importance of cladogenesis, dispersal, and extinction for explaining the observed biogeographic scenario. The j is added to weight founder events/jumping speciation events at cladogenesis (Matzke, 2013b). DIVAlike represents the likelihood interpretation of parsimony DIVA, built by Ronquist (1997). This model emphasizes dispersal and vicariance events. Likewise, BAYAREAlike is the likelihood interpretation of the Bayesian DIVA from Landis et al., (2013). This model integrates only dispersal and extinction events. Then, it tests the influence of cladogenesis on the dataset when comparing it with DEC. We implemented standard model testing, using LRT and AIC, to compare models. The analysis was set at maxareas = 6.

Relative frequencies of ancestral ranges reconstructed for each node were summarized and plotted onto the maximum clade credibility tree from the dated Bayesian analysis performed in Beast.

Trait evolution — The estimation of ancestral state reconstruction was developed using a continuous-time Markov chain model (Mk model). We used "phytools" for comparative biology as implemented in R (Revell, 2012) for the estimation of ancestral character states for discrete and continuous traits using the tree from the integrated IQ-TREE analysis. For example, the discrete trait of substrate had three character states: soil (terricolous plant), rock (saxicolous plant), and tree (epiphyte). We used the ace function that estimates ASR using maximum likelihood (Pagel, 1994) with an equal rate (ER) for the transition rate among character states. For ancestral character estimation for continuous characters, e.g., the ratio of the basal cells in relation to leaf length, we used contMap function to map the states at internal nodes using ML and then interpolated the states along each edge using the equation in Felsenstein (1985; Revell and Freckleton, 2013).

We used the phylogenetic ANOVA (Garland et al., 1993) to test whether the proportion of basal cells was significantly different among each substrate. Subsequently, we conducted a post-hoc test to compare the means among groups of plants from different substrates (p-values by phylogenetic simulation).

Results

Phylogenetic analyses — The concatenated alignment of the target region sequences contained 72,263 molecular characters, from an average of 354 loci (i.e., nuclear exons) per taxon. The integration of molecular and morphological datasets yielded the phylogenetic tree shown in Fig. 2.3, in which *Syntrichia* is a monophyletic group, its closest relatives are *Tortula, Hennediella, Dolotortula,* and *Chenia*, and its more distant relatives are *Saitobryum, Barbula, Leptodontium, Trichostomum,* and *Streblotrichum. Syntrichia flagellaris* was resolved to be outside of *Syntrichia*. We identified 10 well-supported subclades within *Syntrichia*, most of which were geographically or morphologically coherent. *Willia* Müll. Hal., *Streptopogon* Wilson ex Mitt., and *Sagenotortula* R.H. Zander were nested within *Syntrichia* based on the integration of molecular and morphological and the molecular dataset alone.

The analysis of morphological data alone yielded a best ML tree with a log-likelihood of -2,360.3 (Appendix B3, A), while the molecular data alone yielded a best ML tree with a log-likelihood of -438,804.8 (Appendix B3, B). We compared the topology and agreement of clades between the separate datasets and the integrated phylogeny. The tree derived from the molecular data alone agreed with the integrated phylogeny in all the major clades and topology; only *S. rubella* and *S. pagorum* were placed differently.

The tree derived from the morphological data alone differed considerably from the molecular or integrated phylogenies. In that tree, *Syntrichia* was not a monophyletic group because some close relatives, such as *Hennediella, Chenia,* and *Dolotortula*, were nested inside it (although weakly supported). *Tortula* and *S. flagellaris* were sister to *Syntrichia*. Four major clades of *Syntrichia* agreed with the molecular tree or integrated tree, while the other major clades were only partially in agreement with the molecular or integrated phylogeny (indicated by * in Appendix B3).

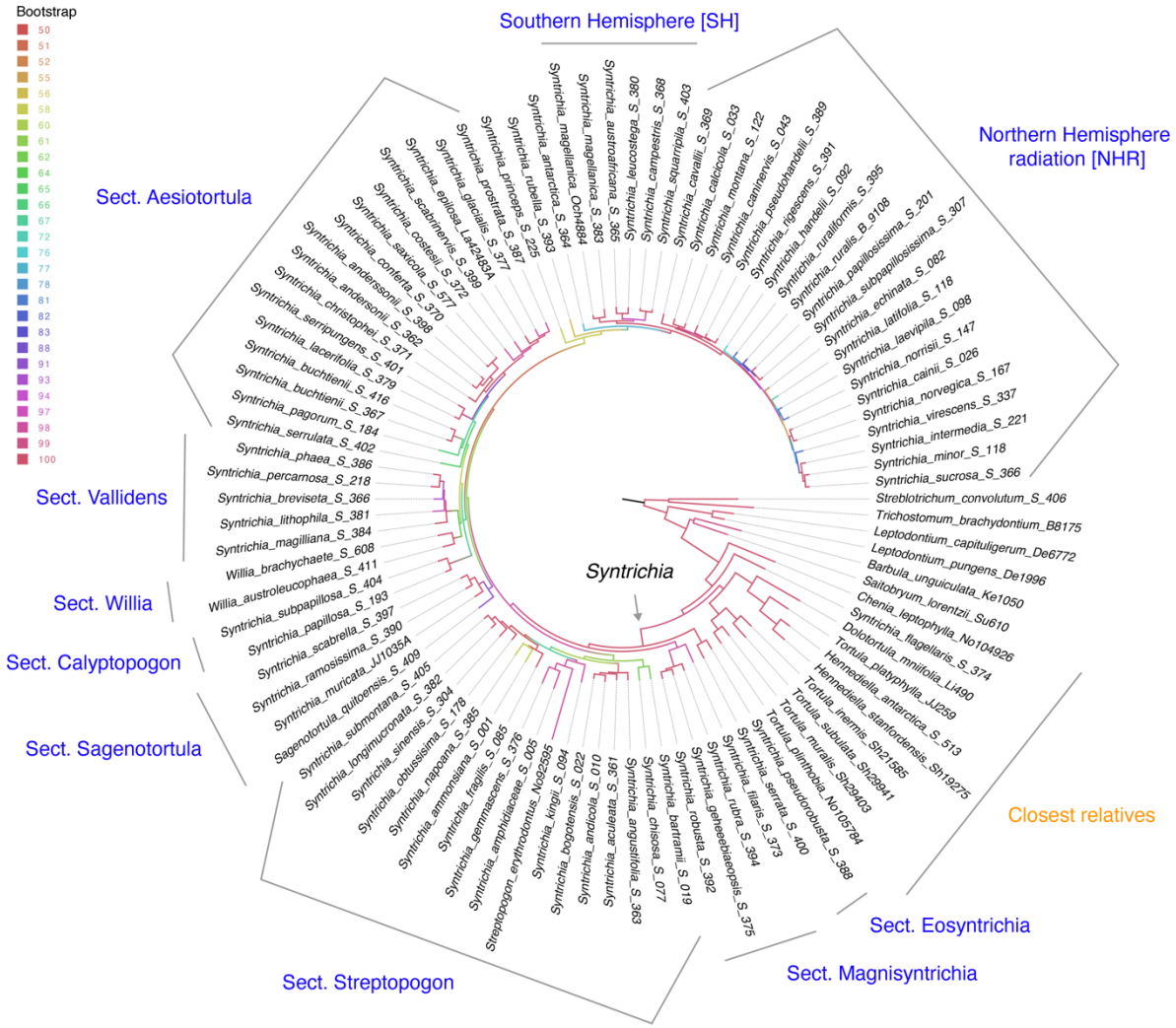

Figure 2.3. Phylogenetic tree of *Syntrichia* and its closest relatives from maximum likelihood analysis of the integrated dataset. All major clades have >90% ultrafast bootstrap support. Names in blue represent the names of the major clades, using the sectional classification of Brinda et al. 2021 plus two informal clade names for the Southern Hemisphere (SH) and Northern Hemisphere radiation (NHR). Colored branches represent the ultrafast bootstrap support ranging from deep orange (50%, very low support) to magenta (100%, high support).

Calibration — We used the tree from the integrated dataset for the calibration of the phylogeny. The calibration estimated at deeper nodes had wider estimated intervals (95% HPD) than the estimations at more recent nodes (Fig. 2.4). The age of the clade *Syntrichia* was estimated at 50.1±6.3 mya (early Eocene). *Syntrichia*'s closest relatives diverged from it around 73.6±9.3 mya. The node for the most distant relatives included in this analysis, i.e., Rhabdoweisiaceae, was estimated at 74.2±8.2 mya.

Within *Syntrichia* deeper nodes that contain some epiphytic and saxicolous clades (e.g., sect. *Streptopogon*) diverged around 39±4.9 mya (see arrow in Fig. 2.4). The largest South

American clade (sect. *Aesiotortula*) was estimated at around 30.1±3.9 mya (see arrow in Fig. 2.4), while the major Northern Hemisphere clade (NHR) was estimated at 13.6±1.8 mya (Miocene) (see arrow in Fig. 2.4).

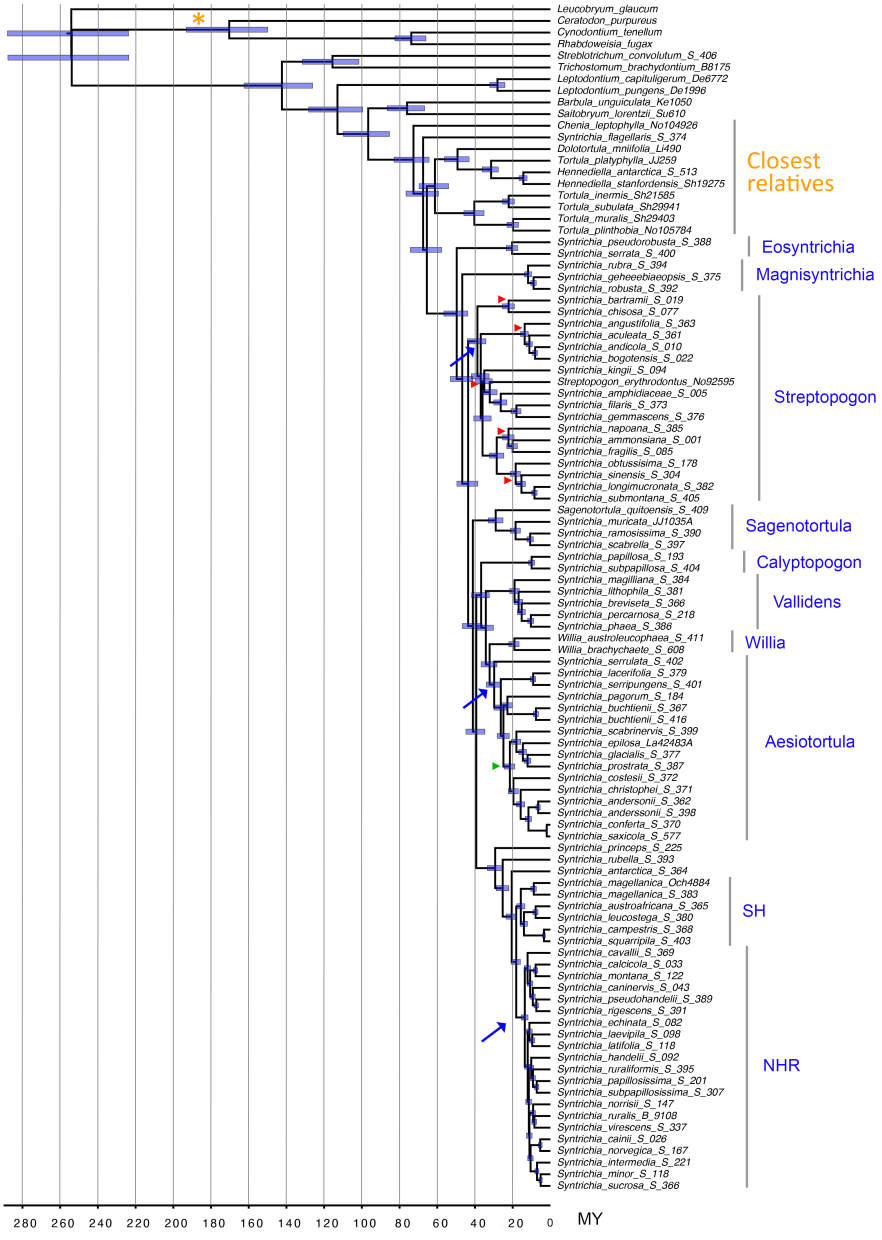

Figure 2.4. Ultrametric tree of *Syntrichia* and its relatives built from the Bayesian analysis of molecular data alone. Names in blue represent the names of the major clades, using the sectional classification of Brinda et al. (2021) plus two informal clade names SH: Southern Hemisphere and NHR: Northern Hemisphere radiation. The orange asterisk (*) represents the calibration point. Red triangles within sect. *Streptopogon* represent important sub-clades discussed in the text. Green triangles within sect. *Aesiotortula* represent an important sub-clade discussed in the text. The three blue arrows indicate the nodes of sect. *Streptopogon*, sect. *Aesiotortula*, and the NHR, respectively.

***Biogeographic history* —** The BAYAREAlike model was favored with six unconstrained areas based on the likelihood ratio test (LRT) and AIC values (Appendix B4). This biogeographic model emphasizes dispersal as a way to explain the observed biogeographic pattern. The ancestral range estimation and divergence time at each node on the phylogeny of *Syntrichia* and its relatives revealed several novel biogeographic patterns (Fig. 2.5). Based on the ancestral range reconstruction, it is likely that *Syntrichia* originated in South America in the early Eocene. Since the closest relatives of *Syntrichia* are distributed predominantly in South America, it is likely that they also have their origin in this continent. However, there is a high degree of uncertainty about the more distant relatives of *Syntrichia* because of their worldwide distribution.

Syntrichia appears to have reached the Northern Hemisphere via long-distance dispersal in two distinct time periods. The first occurred at the divergence time of sect. *Streptopogon* around 44–34.1 mya. The second occurred at the divergence of the major Northern Hemisphere clade, (see NHR in Fig. 2.4) (15.4–11.8 mya). In between these two time periods, two large clades (sect. *Aesiotortula* and SH) diverged within South America (Fig. 2.5).

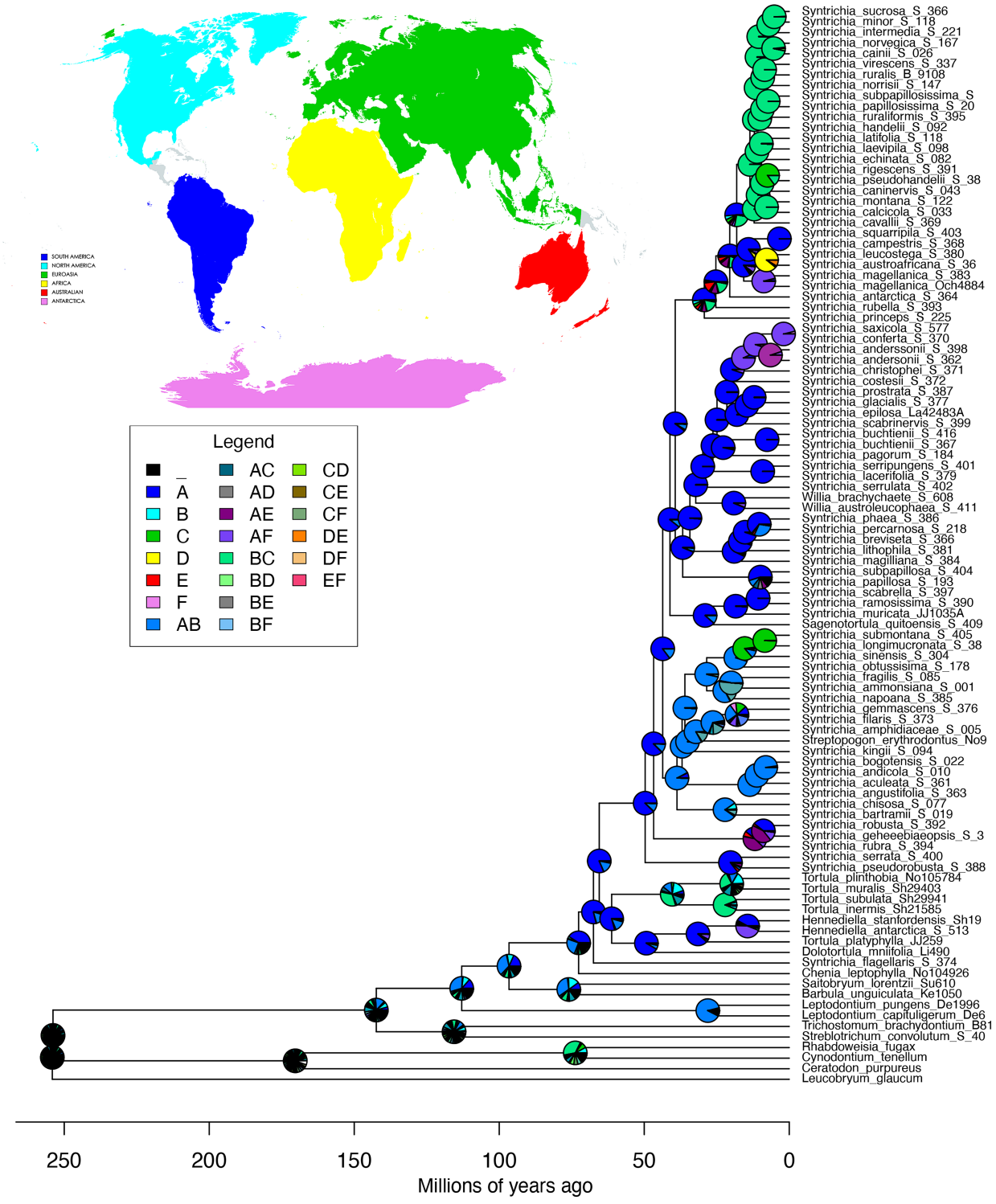

Figure 2.5. Ancestral Range Estimation of *Syntrichia* and its closest relatives on the time-calibrated tree using the BAYAREAlike model (BioGeoBEARS). Pie charts at the nodes indicate the probability of support for respective areas. A: South America; B: North America; C: Eurasia; D: Africa; E: Australasia; F: Antarctica.

Trait evolution **—** *Syntrichia* presents substantial variation in substrate preferences compared to its closest relatives. Saxicolous and terricolous species account for ~30% and ~40% of the total, respectively. In contrast, its closest relatives, *Tortula* and *Hennediella*, are specialized terricolous taxa. Based on our maximum likelihood estimation of the ancestral discrete character, it is likely that *Syntrichia* had terricolous ancestors (Fig. 2.6). However, the ancestral substrate condition deeper in the tree is highly uncertain – each substrate is equally probable. It is estimated there was a switch from terricolous to saxicolous at some deeper nodes of *Syntrichia* (e.g., sect. *Streptopogon*), while the same transition occurred within more recently diverged clades as well, including the major North Hemisphere clade (NHR).

The proportion of basal cells in relation to the leaf length is highly variable in *Syntrichia* (Fig. 2.7, A), while there is less variation of this character among its closest relatives. These outgroup taxa do not have the distinctly differentiated, enlarged basal cells of *Syntrichia* (Fig. 2.7, A, red mapping). The ancestral reconstruction of this continuous character estimated a medium value of the proportion of basal cells (~25-30% of basal cells in relation to leaf length) across deeper nodes in *Syntrichia* (Fig. 2.7, A, light green mapping). However, there are some scattered small clades in the phylogeny that have a larger proportion of basal cells. In some cases, basal cells cover up to almost half of the leaf lamina (~40% of basal cells) (Fig. 2.7, A, light to deep blue mapping). Likewise, some other smaller clades within sects. *Streptopogon* and *Calyptopogon* have a small proportion of basal cells (Fig. 2.7, A, red mapping).

Based on the phyAnova test for the proportion of basal cells within the *Syntrichia* clade (Fig. 2.7, B), there was a significant difference in the proportion of these cells between terricolous (~30% of basal cells on average) and epiphytic (~14% of basal cells on average) plants, while saxicolous plants are intermediate (~25% of basal cells on average) and not significantly different from terricolous plants, although there is a significant difference between saxicolous and epiphytic plants.

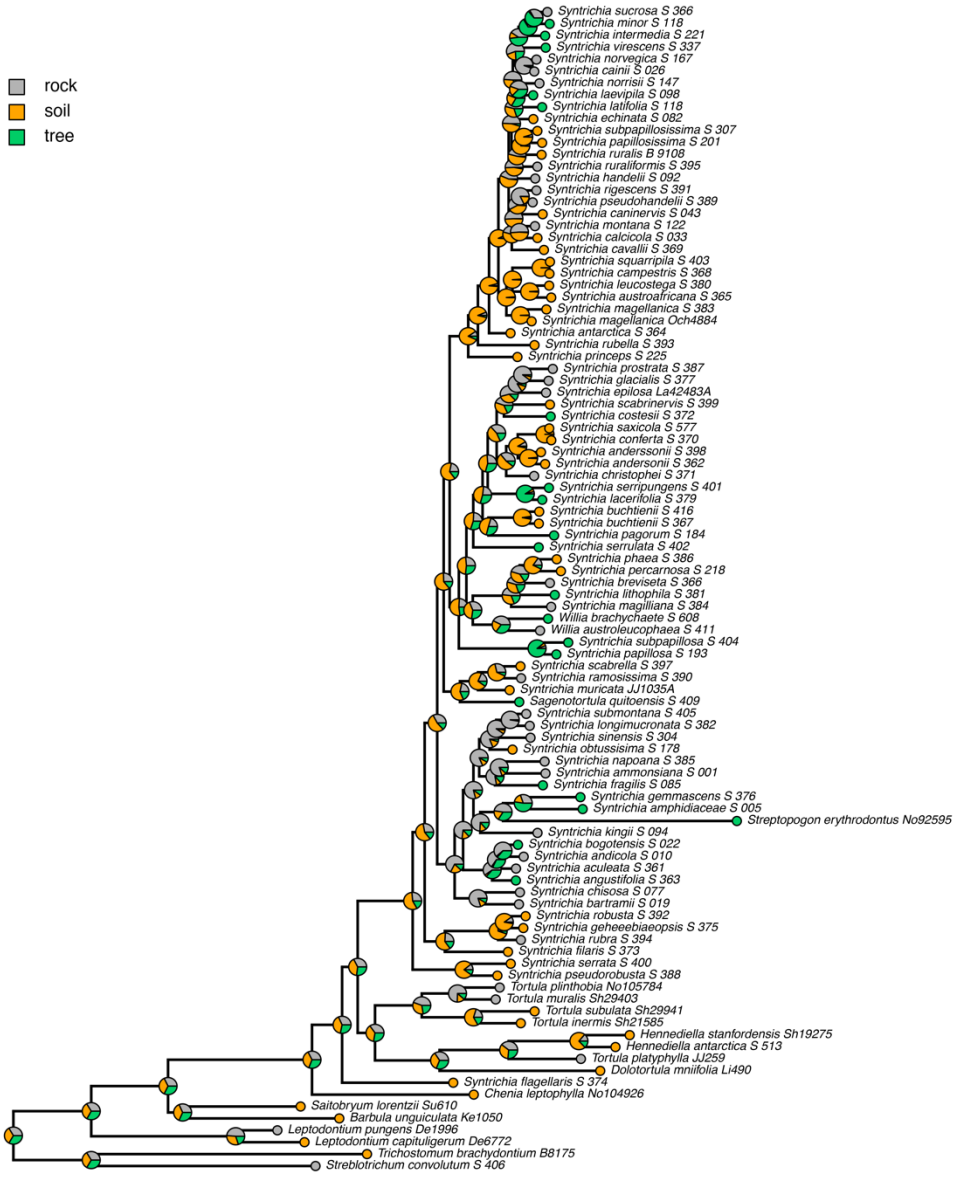

Figure 2.6. Ancestral character reconstruction of a discrete trait (substrate) in *Syntrichia* using an ER model of evolution. States are soil, rock, and tree.

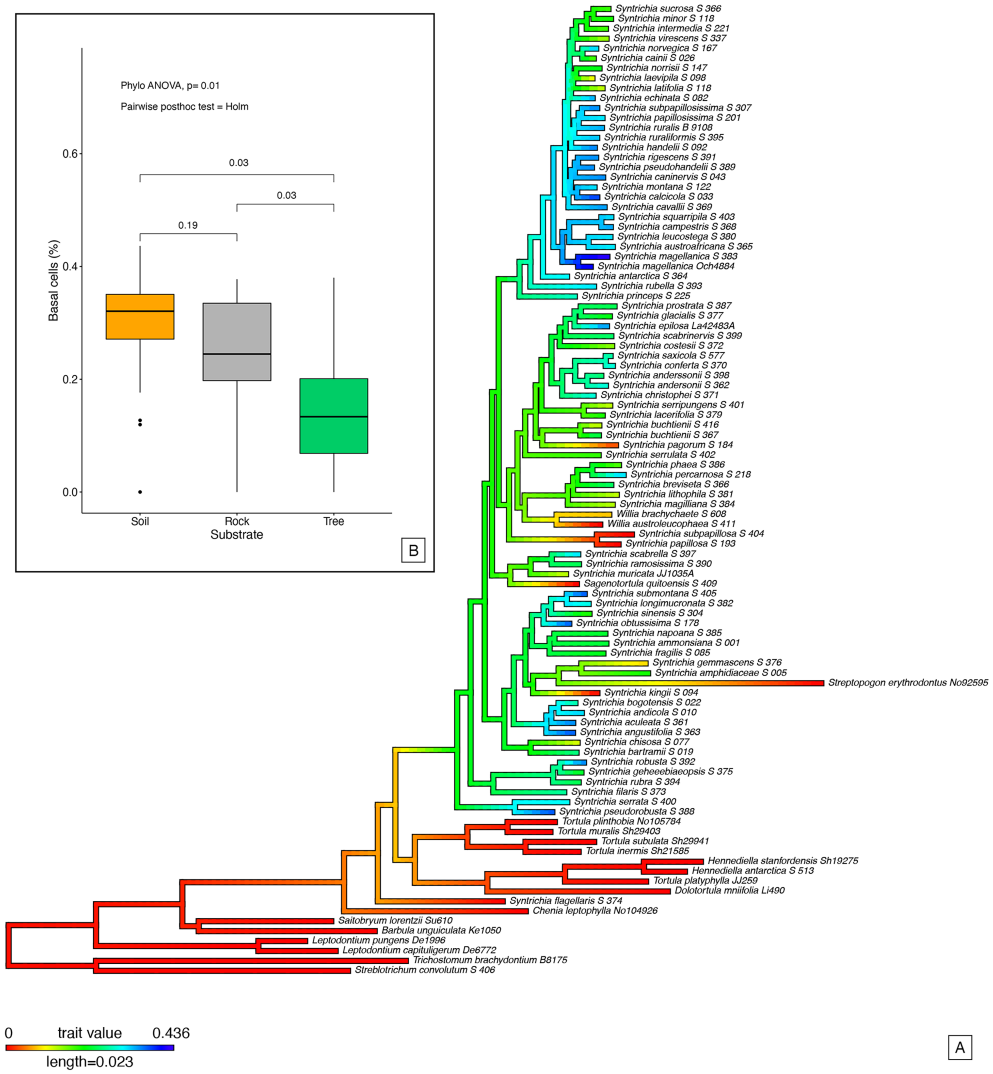

Figure 2.7. A. Ancestral character reconstruction of a continuous trait, proportion of the leaf lamina composed of basal cells (abrupt differentiation between basal and laminar cells), in *Syntrichia* using an ER model of evolution. B. Box plots for the proportion of basal cells (%) according to the substrate (soil, rock, and tree). PhyloANOVA test indicated that the proportion of basal cells differs significantly among the substrate condition (p= 0.001). The subsequent pairwise posthoc test using method holm indicated that the proportion of basal cells from terricolous plants on average was significantly larger than epiphytic plants (p=0.03), while this difference was not significant (p=0.19) between terricolous and saxicolous plants. The proportion of basal cells for saxicolous plants was significantly larger than epiphytic plants (p=0.03).

Discussion

The monophyly of Syntrichia and its taxonomic implications — Our purpose here was not to propose a new taxonomic classification of *Syntrichia*; instead, we applied names to the major clades within *Syntrichia* following the recent classification in Brinda et al. (2021). We applied the name *Syntrichia* to a large and well-supported clade (100% bootstrap support) that consists of 10 major subclades (Fig. 2.3), eight of which correspond to the sections treated by Brinda et al., (2021), and we use those sectional names here.

Our results confirm that the previously accepted genera *Streptopogon* Wilson ex Mitt., *Willia* Müll, and *Sagenotortula* R.H. Zander are nested within *Syntrichia*, as suggested by other recent phylogenetic studies (Mishler et al., in prep). Following Brinda et al. (2021), these genera are treated here as sections of *Syntrichia*. *Calyptopogon* (Mitt.) Broth., is another genus suggested to be nested within *Syntrichia* (Brinda et al., 2021). Although we did not sample the type species of this taxon, it is likely closely related to *S. papillosa* and *S. subpapillosa* (Mishler et al., in prep). *Syntrichia flagellaris* was resolved as being outside of *Syntrichia sensu stricto*, corroborating its placement in the new genus *Syntrichiadelphus* (Brinda et al., 2021). The first node within *Syntrichia* showed sect. *Eosyntrichia* as sister to the rest of *Syntrichia*. This small clade with two terminal taxa (*S. pseudorobusta* and *S. serrata*) shares uncommon characters compared to the rest of *Syntrichia*. They are relatively large plants with lanceolate leaves that are squarrose when fully hydrated, with prominent toothed margins, large sheathing base, and a short mucronate apex (Brinda et al., 2021). With a smaller sampling, Gallego et al., (2014) also recovered *S. pseudorobusta* as an early-diverging lineage, distant to the Neotropical taxa. Another early-diverging clade is sect. *Magnisyntrichia*, which shares several morphological characters with sect. *Eosyntrichia*. However, it is distinct in having irregularly and less strongly toothed margins along the upper portion of the leaf (Brinda et al., 2021), similar to some species of *Hennediella*. These two clades were clearly recovered by both the molecular and morphological datasets (Appendix B3).

Another deeply diverging lineage in *Syntrichia* is sect. *Streptopogon*, which contains *S. erythrodontus*. It is one of the three largest clades of *Syntrichia* in terms of species richness (17 terminals) and one of the most heterogenous. It contains five smaller, ecologically well-supported clades (see red triangles in Fig. 2.4). One of these is a small clade from the Chihuahuan desert of North America (Mishler et al., in prep.). A second clade contains *S. bogotensis, S. angustifolia, S. aculeata,* and *S. angustifolia* and is very distinct morphologically from its sister lineages, with large stems and leaves, a greater proportion of basal cells, and a mucronate hairpoint. In addition, the members of this clade are characterized by inhabiting high elevation areas of the Andes of South America to the mountains of Mexico. The morphological dataset also recovered it as a distinct clade. A third clade contained species that are mainly saxicolous, especially on calcareous rocks and soil (e.g., *S. sinensis*). The remaining two clades consisted of well-known epiphytic or saxicolous species that often produce vegetative propagules in the form of gemmae, brood leaves, or leaf fragments (Zander 1993, Mishler et al., 2007). Despite the atypical morphology found in these smaller clades (i.e., *S. erythrodontus, S. amphidiacea* and *S. gemmascens),* they all produce multicellular gemmae, a character that clearly unified this clade (see a detailed explanation in Brinda et al., 2021).

Clades especially concentrated in the Southern Hemisphere are sect. *Willia*, sect. *Vallidens*, sect. *Aesiotortula*, along with another that is close to the *ruralis*-complex that we informally name

SH here. Section *Willia* forms a robust clade within *Syntrichia* based on both the molecular and morphological phylogenies. Similar leaf ornamentation, presence of hairpoint, strong leaf constriction, and differentiation of perichaetial leaves unite this clade. Section *Vallidens* was a robust clade (100% bootstrap) as well, characterized by small blackish plants with a robust costa with a strong stereid band (sometimes armed with prorae), plane leaf margin, and the presence of a mucro or awn at the tip of the leaf (Brinda et al., 2021). Section *Aesiotortula* was the third-largest clade in terms of richness (16 terminals) and was entirely restricted to temperate regions of South America, except for the widespread species *S. pagorum*. The SH clade contained soil-dwelling species from dry areas of Chile and South Africa and was sister to the largest Northern Hemisphere clade (NHR). *Syntrichia princeps*, the common synoicous species from Western North America, was sister to both the SH and NHR clades. We suggest that *S. princeps* does not occur in South America as previously mentioned by Gallego et al. (2009, 2011). It is likely that the putative *S. princeps* from South America corresponds to a member of SH such as *S. squarripila* or *S. campestris,* since these taxa are superficially similar. Given the taxonomic complexity of this clade, we suggest further taxonomic and molecular studies with denser sampling.

The NHR clade was the largest in terms of richness (21 terminals) and is characterized by its broad ecological amplitude, ranging from desert to alpine meadows in the Northern Hemisphere, especially North America (Mishler, 2007). This clade contains the well-known, model species *S. caninervis* and *S. ruralis*. Since we only sampled one representative of each taxon, understanding the finer evolutionary relationships among these terminals was beyond the scope of this study. Morphological relationships are not completely resolved, and overlapping characters exist among the members of this clade. Therefore, further global study of this clade and its close relatives is needed to understand its recent evolutionary history and proper taxonomy.

While morphological analysis alone yielded a tree that does not align well with current generic concepts, morphology still had a positive impact on phylogenetic support when analyzed in combination with molecular data. For instance, the molecular tree suggested *S. rubella* and *S. pagorum* as a weakly supported clade while the morphological tree included *S. pagorum* with *S. papillosa* and *S. subpapillosa* because of shared leaf shape, ornamentation of the costa, and vegetative propagules (Appendix B3). The integrated tree placed *S. rubella* with increased support as sister to the SH and NHA clades. Nevertheless, the trees from the integrated and molecular datasets in this study were very similar (Appendix B3). Other phylogenetic studies that incorporated a larger genomic dataset and only a few morphological characters found that genomic data largely dictated tree topology (Rota-Stabelli et al., 2011; dos Reis et al., 2012), and tracing results of the evolution of phenotypic characters on the combined or molecular tree revealed similar reconstructions. Even so, having morphological characters coded explicitly into a matrix is better than ad hoc mapping of morphology onto a molecular tree. Integrating morphological characters into phylogenetic analyses remains fundamental for tracing the evolution of phenotypic characters and revealing suites of phenotypic apomorphies to define clades and remains vital for incorporating fossils when tip-dating trees (Lee and Palci, 2015).

Out of southern South America to the rest of the world — The ancestral range reconstructions and estimates of divergence times on the phylogeny of *Syntrichia* and its relatives showed some important biogeographic patterns. *Syntrichia* exhibits three different patterns of intercontinental disjunct distributions, following the descriptions by Wen and Ickert-Bond (2009): (1) between North and South America (Amphitropical disjunction); (2) between Mediterranean climate regions of Eurasia and western North America (Madrean-Tethyan disjunction); and (3)

classic southern Gondwanan disjunctions. Our results showed that these disjunct distributions are best explained by a model (BAYAREAlike) that emphasizes dispersal instead of vicariance as the primary biogeographic mechanism.

Our ancestral range reconstruction suggests that *Syntrichia* originated in South America during the early Eocene (56–44 mya). The two deepest nodes and the distribution of the closest outgroups, support this divergence in time and place of origin (Fig. 2.5). First, sect. *Eosyntrichia*, with a relatively small current diversity (*S. pseudorobusta* and *S. serrata*) is restricted to South America and Australasia. Second, sect. *Magnisyntrichia* is also restricted to South America and Antarctica. It is possible that a dispersal event occurred between South America and Australasia (Fig. 2.5). Although the directionality is still uncertain, the most recent common ancestor of sects. *Magnisyntrichia* and *Eosyntrichia* likely had a South American origin. The transition from late Palaeocene to the early Eocene (~50 mya) was marked by a warm and moist global climate, a predominance of forested ecosystems, and a low equator to polar temperature gradient (Utescher and Mosbrugger, 2007). We hypothesize that *Syntrichia* evolved under an evergreen vegetation dominated by *Araucaria, Podocarpus*, *Nothofagus*, and a few other angiosperm families (Myrtaceae, Myricaceae, and Loranthaceae) in the Southern Hemisphere (Truswell, 1990).

The divergence times of clades that contain South American, South African, or Australasia taxa are much younger than the break-up of Gondwanaland (a continuous process from 140 to 30 mya) (Seton et al., 2012). For instance, the split of the clade that contains *S. leucostega* or *S. austroafricana* from its closest relatives from South America was between 16 to 12.1 mya. A similar case is found in sect. *Vallidens*, in which a single dispersal event from South America may have produced the isolated species *S. magilliana* in South Africa. The predominant direction of dispersal appears to have been from South America to South Africa. Some studies of Neotropical vascular plants argued that long-distance dispersal was the most plausible mechanism for the Gondwana-like pattern in which birds served as a vector (Givnish et al., 2004; Nie et al., 2012). In contrast, the similarity among temperate spore-bearing plants from Southern Hemisphere landmasses has been explained by anisotropic (direction-dependent) transport along with prevailing winds (Muñoz et al., 2004). Thus, we hypothesize that long-distance dispersal in *Syntrichia* between southern South America and Africa might have been driven by the West Wind Drift as with other plant groups (San Martin et al., 2007).

We suggest that South America represented not only a place of origin, but also an area for diversification. When *Syntrichia* reached new areas, in some cases, it adapted to new microhabitats, such as trees or specialized rock substrates, or even the punas of the Andes in South America. For instance, the small clade that contains *S. andicola* and *S. bogotensis* diversified less than 15.8–11.7 mya at high altitude (>2,200 m) along the Andes of South and Central America, as far north as the high volcanoes in Mexico (Mishler, 2007), probably via stepping stones. On the other hand, several clades remained in South America and diversified there (e.g., sect. *Aesiotortula*). We observed a higher frequency of epiphytic or saxicolous plants in these lineages compared to the deeper nodes represented by sects. *Eosyntrichia* and *Magnisyntrichia* (Fig. 2.6).

The late Oligocene through Miocene (28 to 7 mya) contained a series of major events that profoundly affected the biota of the Southern Hemisphere. First, oceanic incursions that had fragmented the distribution of many taxa in South America began to withdraw. Second, the Andes began to rise significantly, creating new cold and alpine habitats and a rain shadow effect that drastically reduced the annual precipitation alongside of the Andes (Hoorn et al., 2010; Simpson, 2014). Lastly, there was significant global cooling and increasing aridity due to ocean circulation changes. By the late Miocene, a mosaic of temperate forest, matorral, Patagonian steppe, and

grassland began to dominate (Willis and McElwain, 2014). Due to these changes in topography and climate, the period from late Eocene (~40 mya) to Miocene (~5 mya) may represent the time of highest plant diversity in the Neotropics (Wilf et al., 2003; Liu et al., 2020; Luebert and Weigend, 2014), and *Syntrichia* might represent one case of a moss clade diversifying there. Currently, *Syntrichia* is one of the largest genera of the Pottiaceae in the tropical Andes (Churchill et al., 1995; Churchill, 2009) and the second-largest genus in terms of species richness of all reported mosses in Chile (Müller, 2009).

Amphitropical disjunct distributions are common biogeographic patterns among vascular plants (Raven, 1963; Moore et al., 2006), but are less commonly reported in bryophytes. We estimate that a few separate dispersal events occurred from the Southern Hemisphere to the Northern Hemisphere. A few other dispersal events occurred more recently to reach South Africa or Eurasia. Around 44–34 mya, *Syntrichia* expanded its distribution to reach the Northern Hemisphere by dispersal of several clades, e.g., in sect. *Streptopogon*. For instance, there was a dispersal event from South America to the Northern Hemisphere (32–25 mya), by the clade containing S. *longimucronata*, *S. submonata, S. sinensis,* and *S. obtusissima,* which diverged after that date. Other examples of amphitropical disjunctions in mosses suggest a more bipolar pattern. The endemic moss *Tetraplodon fuegianus* from southern South America has its closest relatives in North America, showing a classic disjunct bipolar distribution (Lewis et al., 2014). Lewis et al. (2017) showed that this species originated by a single long-distance dispersal from a population in North America involving birds as dispersal agents. This bipolar pattern is also observed in the moss *Arctoa fulvella* (Ochyra and Buck, 2003).

The most striking and recent long-distance dispersal event from South America to Northern Hemisphere occurred around 15.4–11.8 mya. This event resulted in a recent diversification of the Northern Hemisphere clade that we refer to here as the NHR (the Northern Hemisphere Radiation), for which the sister group is South American. Despite similar morphologies between members of the SH and NHR, which lead to frequent misidentifications in herbaria and the literature (see the previous section), the NHR appears almost completely restricted to the Northern Hemisphere. Later dispersal events likely occurred from North America to Eurasia as the NHR clade diversified. Recent dispersal events around the northern hemisphere have been reported in other groups of mosses. Shaw et al. (2003) reported molecular and morphological differentiation among *Claopodium whippleanum* (Sull.) Renauld & Cardot, *Dicranoweisia cirrata* (Hedw.) Lindb. Ex Milde, and *Scleropodium touretii* (Brid.) L.F. Koch associated with their disjunct distribution between the Old and New World and concluded that recent long-distance dispersal has occurred in all three taxa.

The NHR encountered new habitats ranging from desert to alpine meadows as the expansion of drier ecosystems and mountainous formations accelerated in the Northern Hemisphere during the Late Miocene (Herbert et al., 2016). For instance, *S. caninervis*, *S. ruralis*, and *S. papillosissima* are widely distributed and co-occur in desert or steppe ecosystems (Mishler, 2007). *Syntrichia caninervis* is a dominant moss in dryland areas from the Mojave Desert in the United States (Bowker et al., 2000) to Gurbantünggüt in China (Zheng et al., 2011), while *S. norvegica* is only found at high altitudes in the subalpine and alpine. In addition, *Syntrichia latifolia* and *S. laevipila* are epiphytic taxa that apparently diversified after dispersal to North America (Gallego, 2005).

Given the recent origin of the NHR clade, with short branches in the phylogeny associated with an apparently rapid increase in diversity, morphological disparity, and new ecological preferences, we suggest this may be a rare example of adaptive radiation in mosses. The timing of

the radiation is in agreement with the global cooling of the oceans and mountain building (Willis and McElwain, 2014). These episodes contributed to a general trend of increasing aridity and marked seasonality in North America (Ruddiman and Kutzbach, 1989) that forced the appearance of new ecosystems between Oligocene and Pliocene (~34–2.5 mya; Herbert et al., 2016) that are still present today. In the light of these global climatic and topographical shifts, it appears that the NHR radiated during the transition of sub-tropical forests to grassland, savannas, or Mediterranean-type vegetation in the Northern Hemisphere from the beginning of late Miocene (11.6–5.3 mya). This adaptive radiation hypothesis needs to be tested further, and our group is working on this with greater sampling from the Northern Hemisphere.

The current distribution of *Syntrichia* has resulted from several factors, including dispersal, wide ecological range and tolerance, and potential adaptations to new environments. *Syntrichia* clearly began its diversification in South America, and then later dispersed to other southern continents and the Northern Hemisphere. The genus experienced major diversification events first in South America and later in the Northern Hemisphere (especially North America), the areas with the current greatest species richness.

Habitat associations with water-related traits — Ancestral character reconstruction in *Syntrichia* showed that it has a higher ecological amplitude and greater disparity of morphological characters than its closest relatives. Almost all its closest relatives inhabit soil substrates, lack asexual propagules (except *Chenia leptophylla*), and do not have the same cellular organization and abrupt distinction between basal and laminar cells (Mishler, 2007) as found in *Syntrichia*. *Syntrichia* appears to have had predominantly terricolous ancestors at the deeper nodes (e.g., sects. *Eosyntrichia* and *Aesiotortula*), but at more recent nodes (e.g., within sects. *Aesiotortula* and *Streptopogon*) shifts occurred to either saxicolous (e.g., the sub-clade that contains *S. glacialis*) or epiphytic (e.g., the sub-clade that contains *S. erythrodontus*) habitats (Fig. 2.6).

The ancestral conditions for *Syntrichia* appear to be a moderate area of the leaf with elongated basal cells (Fig. 2.7), absence of asexual reproduction (Appendix B5), dioicous sexual condition (Appendix B6), a well-developed hairpoint (Appendix B7), and hydroids present (Appendix B8). We estimated several shifts to other character states for each trait, especially within larger clades (sect. *Streptopogon*, sect. *Aesiotortula*, and the NHR). For instance, transitions to having larger proportions of basal cells occurred within both NHR and SHs. Some internal nodes within sect. *Aesiotortula* shifted to a reduced extension of the costa as a mucro or short awn, from the ancestral condition of having a well-developed hairpoint.

We suggest that some traits analyzed in this study are related, at least in part, to water relations. One of the most striking correlations was found between the proportion of basal cells and the substrate condition. Although *Syntrichia* had terricolous ancestors, it shifted to saxicolous or epiphytic conditions several times (i.e., within sect. *Streptopogon*, sect. *Aesiotortula*, sect. *Calyptopogon*, and the NHR). This transition occurred in parallel with the reduction in plant size and rudimentary development of the basal cells (Fig. 2.6 and Fig. 2.7). Terricolous lineages have an abrupt transition between basal and laminar cells in which basal cells are more elongated and are perforated. These perforated basal cells are thought to be involved in rapid external water transport and storage. The presence of hyaline cells (dead and porose), as found in other mosses (e.g., *Sphagnum* and *Leucobryum*), significantly increases water storage (Proctor, 1979). All Pottiaceae members have differentiated basal cells to some extent, but most are not as large, distinct, and perforated as in *Syntrichia*.

Epiphytic lineages in *Syntrichia* are characterized by small plants, bulbiform leaf arrangement when dry (Fig. 2.2), a short extension of the costa, presence of asexual propagules, and reduced size of basal cells. In some other unrelated mosses, this phenomenon has been called the "epiphytism syndrome" to characterize plants with a distinct morphology (Fedosov et al., 2021), including mostly a differentiation of perichaetial leaves (Tubanova et al., 2019) and/or distinct ornamentation of peristome (Vanderpoorten et al., 2002), associated with a transition to epiphytic conditions (Fedosov et al., 2021). We observed diversification of habitat preferences within several clades of *Syntrichia* and associated water-related traits, especially the proportion of basal cells in the leaf, also transitioned independently multiple times in the phylogeny, possibly due to convergence. However, the way these characters function and/or reflect adaptation to different environmental regimes is an area that remains poorly understood, and careful analysis from different lines of evidence is required in the future.

Conclusions

Our study is the first to present a well resolved species-level phylogeny of *Syntrichia*, including the vast majority of named species, in order to provide a robust evolutionary framework for future research on this group of mosses and its closest relatives. The complex history of disjunct distributions observed in this clade (Amphitropical, Madrean-Tethyan, and Gondwanan disjunctions) revealed that *Syntrichia* reached new landmasses primarily via long-distance dispersal. In addition, South America is an essential biogeographic region for *Syntrichia*, being the major center of diversity and ancestral range for the clade. The region is also the primary source area for dispersal, with several lineages originating in the Andes. We suggest the orogeny of the Andes probably impacted the evolutionary history of bryophytes in South America by providing new niches, refugia, corridors and/or a place of diversification as has also been shown for vascular plants. Based on herbarium collections, there are still large gaps in our knowledge of *Syntrichia* and other mosses ranging from the Andes of Peru to Colombia. Further field exploration is necessary to fully understand the distribution patterns and diversity of the mosses of this region, including *Syntrichia*. We found that *Syntrichia* experienced a notable diversification in the Northern Hemisphere (since ~13 mya) that was roughly coincident with increased aridification (Miocene). Given the poikilohydric and desiccation tolerant nature of *Syntrichia*, we found that water-related traits were often associated with a particular substrate. A more detailed study considering the functional morphology and physiological aspects of the ectohydric traits of each subclade within *Syntrichia* needs to be done to test comparative hypotheses regarding adaptations to different environments. This research has general implications for the origin and diversification of plants with global disjunctions and emphasizes the role of LDD and dynamism in the distribution patterns of bryophytes. Further studies at the population level including greater sampling within the NHR clade are required to clarify the taxonomy, evolutionary history, and local biogeographic patterns within this group.

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Data availability statement

All raw sequence data is archived in NCBI SRA database (BioProject PRJNA853349; Appendix B1). Our files with aligned molecular data, morphological matrix, and trees are archived in Dryad Digital Repository (https://doi.org/10.6078/D1JT6S).

Chapter 3

The dynamics of external water-conduction in the dryland moss *Syntrichia* Brid.

Abstract

Background and Aims: Syntrichia relies on external water conduction for photosynthesis, survival, and reproduction, a condition referred to as ectohydry. In ectohydric species water is absorbed and lost over the entire plant surface, thus much of their structure might relate to water conduction. Capillarity spaces are abundant in *Syntrichia*, but the link between function and morphology is complex. The aim of this study was to investigate whether external conduction and storage is the main source of water for *Syntrichia* and to provide a better understanding of species-specific morphological traits underlying functions of conduction or storage.
Methods: Capillary systems ranging from individual leaf cells to multiple stems at different densities were observed and measured to understand ectohydry. We used SEM, ESEM, and confocal microscopy for observing anatomical characters in several species of *Syntrichia*. We measured hydration/dehydration curves to understand the rate of conduction and dehydration by experimental approaches.
Key results: Syntrichia is an ectohydric moss that can externally transport and store water from the base of the stem using capillary action. We propose a new framework to study ectohydric capabilities, that includes three morphological scales and timing of going from completely dehydrated to fully hydrated. Characters of interest included in this model include: cell anatomy (papillae development, hyaline basal cells, and laminar cells), architecture of a single stem (concavity and orientation), and whole clump features (density of stems). We report significant variation in the speed of conduction, water holding capacity and hydration associated with each species.
Conclusions: All *Syntrichia* species are capable of external water conduction and storage, but the relevant traits differ among species. Furthermore, the capillary pathways differ and morphology changes as the plants wet. These results help to understand potential evolutionary and ecological tradeoffs among speed of water conduction, water holding capacity, ontogeny, and differing habitat requirements. An integrative view of ectohydry in *Syntrichia* contributes to understanding the roles of mosses in the hydrological environment.

Keywords: Ectohydry, capillary system, hydration, dehydration, *Syntrichia*.

Introduction

Terrestrialization imposed major challenges for photosynthetic organisms. The plesiomorphic condition for the earliest land plants, as judged by ancestral character state reconstruction, must have included a moderate form of desiccation tolerance (Oliver et al., 2005; Mishler and Oliver, 2009). *Desiccation tolerance* (DT) is the ability of the plant to revive after being air-dried at the cellular level (Alpert and Oliver, 2002; Proctor et al., 2007; Koster et al., 2010). A related but distinct condition is *poikilohydry*, the rapid equilibration of the plant's water content to the surrounding environment (Kappen and Valladares, 1999; Alpert and Oliver, 2002). After they invaded the land, embryophytes explored two contrasting paths for facing the dehydrating effects of the atmosphere and intermittent water supply (Proctor, 2001; Nicklas, 2016).

The first path, taken by several different lineages of bryophytes (i.e., liverworts, mosses, and hornworts) involved new adaptations to tolerate free water loss rather than prevent it, and to gain water externally rather than internally (Proctor, 1982; Proctor, 2000). Most bryophytes tolerate desiccation by suspending their metabolism when dry and rapidly resuming photosynthesis and growth during moist periods (Proctor, 1979; Proctor, 2001). The plants appear to be completely dead when dry, yet revive after rewatering. The second path, taken by tracheophytes (vascular plants), was to evolve efficient internal machinery to move water from the soil to the canopy (referred to as *endohydry;* Proctor and Tuba, 2002). Vascular plants evolved adaptations to prevent water loss (i.e., a cuticle and stomata closure) and conduct water internally via specialized internal tissues - xylem and phloem from roots that absorb water and nutrients (Proctor, 1982).

While a few moss lineages can be classified as endohydric, the vast majority of mosses are either ectohydric or mixohydric (Buch, 1945; Proctor, 1979). Endohydric species of mosses have well-developed water-conducting cells (WCC) - hydroids - similar to the internal conducting systems of vascular plants (Hébant, 1977; Ligrone et al., 2000). Water is absorbed from the substratum and conducted internally to the evaporative surface (Raven, 2003); a pattern associated with a limited number of large moss species (e.g., *Polytrichum* and *Dawsonia*) (Bobdribb et al., 2020). Ectohydric mosses, on the other hand, rely on external water transport and absorption over the entire plant surface (Proctor, 1979). Water is quickly absorbed and moves rapidly along the plant surface. This character allows moss to take advantage of dew or fog by absorbing water directly from the atmosphere (Anderson and Bourdeau, 1955; Glime, 2007). A combination of a wettable surface with internal conduction is characteristic of mixohydric moss species (Buch, 1945; Proctor, 1982). Indeed, some of the large endohydric species conduct water internally but also through capillary spaces found on the sheathing leaf bases (Proctor, 2009).

External water conduction in ectohydric species requires pathways for water to move from one place to another, without completely covering all cell surfaces in water (which would not allow sufficient gas exchange) (Proctor, 2011). There are a variety of different ways that ectohydric moss achieve water transport. Overlapping leaves with sheathing bases can create a network of capillary spaces. Paraphyllia (small leaf-like structures scattered along the stem), or rhizoids (hair-like filaments on stems that anchor the plant to the substrate), can also increase the surface area and facilitate water transport (Proctor, 2011). In some mosses, interspaces between papillae (tiny projections of the leaf surface) can reduce water tension and create a network of channels for an efficient capillarity movement across the leaf. Finally, the presence of hyaline leaf cells (dead and

porose), found in several moss species (e.g., *Sphagnum* and *Leucobryum)*, significantly increase water storage (Proctor, 1979; Glime, 2007).

Water uptake has been observed in mosses through observations and experimental procedures ranging from simply splashing water on a clump of mosses (Sand-Jensen and Hammer, 2012), to using dyes or radioactive tracers to track water movement in a particular tissue (Sokolowska et al., 2017). Much attention has been centered on endohydric species due in part to their similarity to vascular plants. A few moss groups, such as Polytrichaceae and Mniaceae, have become model systems to study internal water relations in mosses (Bobdribb et al., 2020). However, mechanisms for water uptake, movement, and storage need to be studied in ectohydric species as well, which are the great majority of moss species and furthermore represent a distinctive pathway to life on land as discussed above.

Syntrichia is a monophyletic group of mosses with more than 90 named species distributed in temperate regions worldwide ranging from deserts to alpine habitats (Mishler, 1994; Gradstein et al., 2001; Jauregui-Lazo et al., in prep.). This genus displays an extraordinary diversity of leaf characters, sizes, and shapes (Zander, 1993), which might be related, in part, to water uptake and external conduction. However, relationships between structure and function are complex. As *Syntrichia* acquires water, small chambers and capillary spaces fill up with water and the moss expands, making a completely new set of structural characteristics appear, ranging from modifications in the architecture of the whole plant to extensive changes in leaf stance and cell turgor. There are many capillary systems and frequently found together in the same taxon in *Syntrichia*, which suggests that some characters are interconnected. The way these characters function and/or reflect adaptation to different environmental regimes remains poorly understood.

This study aims to: (1) provide a new framework for understanding the dynamics of external water conduction using the genus *Syntrichia* as a model system, (2) understand the dynamics of hydration and dehydration, and (3) discuss the implications of external water conduction to the overall ecology and life history trade-offs in mosses.

Methodology

Plant material — A total of 11 species of Syntrichia were studied to evaluate different aspects of water relations. Gametophytes of *Syntrichia princeps* (De Not.) Mitt, *S. papillosissima* (Copp.) Loeske, and *S. bartramii* (Steere) R.H. Zander were selected (about 5 stems of each species) for compound, scanning electron, and confocal microscopic observations (each described below). Mosses were hydrated in the laboratory at 12^0C in petri dishes for a week under a photoperiod of 12h day and 12h night. The gametophytes were sprayed three or four times a week with deionized water until further used, however, they were slowly dehydrated before microscopic examinations.

We selected four stems of each of six soil-dwelling species: *S. campestris* (Dusén) R.H. Zander, *S. calcicola* J.J. Amann, *S. caninervis* Mitt., *S. papillosissima*, *S. ruralis* (Hedw.) F. Weber & D. Mohr, and *S. squarripila* (Thér.) Herzog ex Brinda, Jáuregui-Lazo & Mishler; to reconstruct the hydration curves. Only *S. calcicola* was subjected to the dehydration experiment.

We selected seven species of *Syntrichia,* from a variety of substrate preferences, for comparisons of speed of external conduction and holding capacity at full-turgor: *S. amphidiaceae*

(Müll. Hal.) R.H. Zander; *S. papillosa* (Wilson ex Spruce) Spruce; *S. bartramii*; *S. chisosa* (Magill, Delgad. & L.R. Stark) R.H. Zander; *S. calcicola*; *S. caninervis,* and *S. papillosissima*. All stems were randomly sampled from recent herbarium specimens deposited at the University Herbarium at the University of California, Berkeley.

Fine-scale anatomical structures **—** We sampled completely developed leaves from the upper section of the stem. Samples were hand-sectioned with a razor blade for a cross-section of the leaves. We created permanent slides for future use and comparison. We used a Quanta 3D FEG 200/600 machine (from FEI Company, USA) for both scanning electron microscope (SEM) and environmental scanning electron microscope (ESEM) microscopic observations. The setup conditions are detailed in Table 3.1.

Table 3.1. Optimal setting for the scanning electron microscopy (SEM) and environmental scanning electron microscope (ESEM) based on *Syntrichia* specimens.

Vacuum mode	Beam settings (adjustments)	Notes
HiVac (SEM)	Detector: ETD Accelerating voltage: 5-10 [kV] Spot size: 3.5-4.5 Aperture size: 30 [μm] Beam current: 0.01 [nA] Pressure: <10 Pa	The specimen for High Vacuum mode must be able to withstand a low-pressure environment. It must be clean and conductive. We used a coated sample with Argon.
ESEM	Detector: GSED Accelerating voltage: 10-15 [kV] Spot size: 5 - 6 Aperture size: 30 [μm] Beam current: 0.1 [nA] Pressure: ~600 Pa	All the specimens were in fresh state.

Tracers **—** We applied two tracers to observe water uptake, movement, and storage. First, we used methylene blue to increase contrast and visualize the movement of the water when applied to different parts of the moss. We performed the visualization of the perforated hyaline basal cells after 20 min of submerging the moss tissue in a solution of methylene blue.

We sampled dehydrated and well-developed leaves and stems from gametophyte tissue. We exposed these leaves to 1% Lucifer Yellow (LYCH) (ThermoFisher, USA) to detect apoplastic transport as described in Bederska et al., (2012). After the exposure of 10-15 min. with LYCH the tissue was washed with distilled water. The whole leaf and cross-sections were mounted in water and analyzed with confocal microscopy. We used a Zeiss LSM 710 (Carl Zeiss Inc., USA) laser scanning confocal microscope using 10X, 20X, and 40X objectives. The emission spectrum was between 535-575 nm for LYCH. The images from confocal microscopy were processed by Imaris 3-D software (Oxford Instruments, UK) at the Biological Imaging Facility at the University of California, Berkeley.

***Hydration curves* —** We set up a system to apply a predetermined amount of water (1, 3, 8, 15, 30, 70, and 110 μL) to the base of a shoot in order to observe the overall water uptake and movement from the bottom toward the tip of the stem. The stems were at least 5 mm in height, clean, green, and fully developed. We measured the initial and final weight (mg), height (mm), and the vertical distance traveled by water along the stem (mm). We calculated the water content ([[Final weight (wet) - Initial weight (dry)]/ initial weight (dry)] *100) in relation to the dry weight at a given amount of water as suggested by Anderson and Bourdeau (1955). We used a non-linear regression model in R 4.1.0 to plot hydration curves (water content, %dry weight) for each amount of water to compare species.

***Speed of conduction and holding capacity* —** The speed of conduction was calculated by measuring the rate of external water conduction to cover the full height of the stem (from the bottom to the tip) until the moss shoot reaches maximum storage capacity (when the stem and leaves are fully expanded and stop absorbing and distributing water). Then, the holding capacity at full turgor was measured as a water content (% dry weight) at this point as described in the previous section. We used four replicate stems for each species. We compared the mean speed (mm/s) and holding capacity (% dry weight) of the different species using a non-parametric Kruskal-Wallis test. Subsequently, we performed individual comparisons of the means of the mentioned metrics for two independent groups using the Wilcoxon test in R 4.1.0.

***Dehydration curves* —** The effect of density of stems on drying rate was measured by placing individual stems of *S. calcicola* of similar weight and size into a simulated clump. We used a woven stainless-steel mesh of 10mm^2 with 1mm^2 holes to place individual stems. We used three densities with four replicates each. Density one (Clump 1) consisted of 40-50 stems/10mm^2 in which all stems touched other when hydrated (simulating a dense clump); Density two (Clump 2) consisted of 20-25 stems scattered around with minimal proximity when hydrated, and Density three (Clump 3) consisted of 10 stems/10mm^2 scattered with no stems touching when fully hydrated. The clumps were hydrated from their base and placed for slow dehydration in a controlled room (at 12C and 40-60% under a photoperiod of 12h day and 12h night). We used a non-linear regression model in R 4.1.0 to plot the dehydration curve according to dehydration time.

Results

Fine-scale anatomical structures — The leaves of *Syntrichia* are composed of two main types of cells, photosynthetic upper laminar cells, and hyaline basal cells (Fig. 3.1, A). The laminar cell size varies from 5 to 15 μm. The hyaline basal cells are distinct from the laminar cells, since they are clear, elongated thin-walled cells, often with perforated upper and lower surfaces (Fig. 3.1, B). Both sides of the laminar cells have bulging surfaces to a great or lesser extent, and also bear papillae, which are hollow projections of the cell. Together, these cell projections create intercapillary spaces on the leaf surface from 3 to 10 μm wide (Fig. 3.1, C). The ornamentation of laminar cells is species-specific. *S. bartramii* has a relatively flat cell surface and shorter papillae as compared to *S. princeps* or *S. papillosissima*. The cell surface of *S. princeps* is bulging and has numerous forked papillae per cell. In contrast, *S. papillosissima* has an extremely bulging cell surface but only a single large papilla with two successive branching (Fig. 3.1, C).

The initial contact of water with hyaline basal cells and papillae is shown in Fig. 3.1 (D-F) for *S. princeps* (similar observations were made for *S. papillosissima* and *S. bartramii*). The images derived from ESEM suggested that water filled up the hollow spaces of the hyaline basal cells as indicated in light blue arrows in Fig. 3.1 (D). The small spaces among papillae formed a network of capillary spaces where the water began to fill up and distributed along the leaf lamina. The recurvature of the leaf margin was an additional location where the water began to move rapidly and distribute across the leaf.

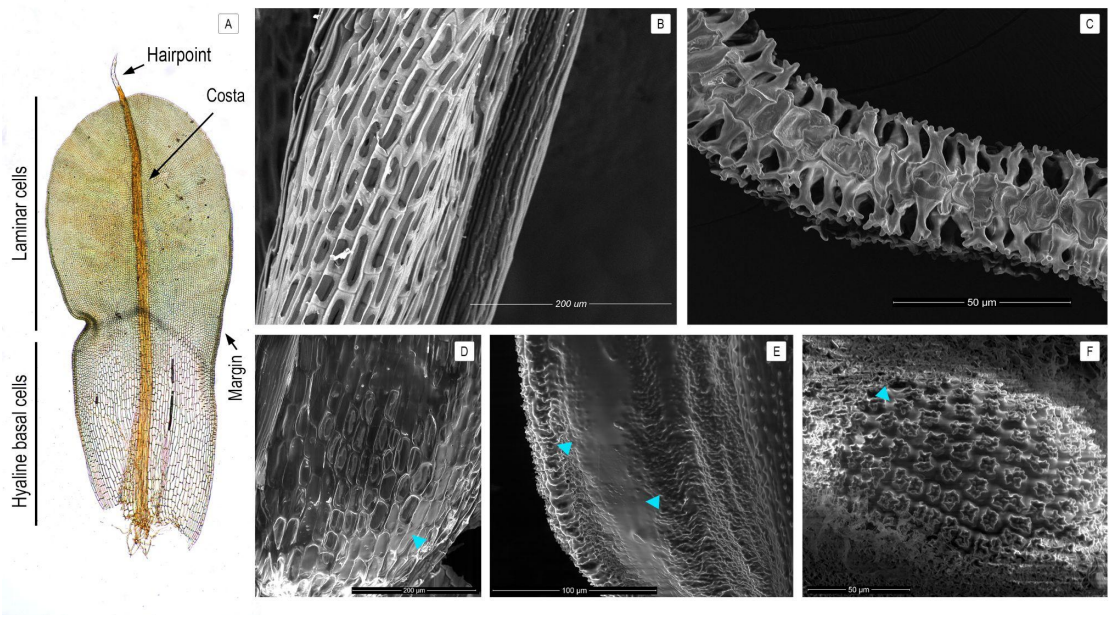

Figure 3.1. A: Leaf top view of *S. princeps* indicating the differentiation between laminar and hyaline basal cells and the hairpoint, costa, and margin. B-C: Scanning electron microscope images of dry *S. papillosissima* to show the elongated and perforated basal cells (B) and papillae in a cross-section (C). D-F: Environmental scanning electron microscope (ESEM) images of wetting *S. princeps* showing the initial stage of hydration in the hyaline basal cells (D), laminar cells (E), and interspaces among papillae (F). Light blue triangles indicate the capillary spaces in contact with the free water.

***Tracers* —** Leaves of *S. papillosissima*, *S. princeps*, and *S. bartramii* were able to absorb and transport the methylene blue and LYCH. Methylene blue was an efficient tracer for observing external water movement in the moss shoot. When water containing the dye was applied to the base of the shoot the water moved upward rapidly. The water first moved externally up to the tip of the stem while moving through and filling up the hyaline basal cells and the spaces among the sheathing leaf bases, rhizoids, and the stem. Then the hydration process began to reach the leaf lamina as the water moved upward on the leaves via the capillary channels described above. In the dry state the folded lamina and recurvate in the margin of the leaf initially absorbed water faster than in other locations of the lamina. As the leaf opened to its wet state, the movement then occurred more generally across the lamina until reaching maximum capacity. Supplementary Information Video 1 shows the hydration of an individual stem in S. *papillosissima*.

Lucifer yellow (LYCH) proved useful to trace hydration in the walls of laminar cells. At full hydration, LYCH was located in the leaf lamina, specifically in the apices of the papillae, and covered the whole hairpoint. LYCH was slightly bound to other parts of the cell, such as the area between the papillae, and associated to the wall of the hyaline basal cells. The processes of external water movement using methylene blue dye and 3-D reconstructions of the reaction between LYCH and the different anatomical characters are documented in separate movies in Supplementary Information Video 2-3.

***Hydration curves* —** An asymptotic non-linear regression curve of hydration of the moss shoots for six *Syntrichia* species (*S. campestris*, *S. calcicola*, *S. caninervis, S. papillosissima*, *S. ruralis*, and *S. squarripila)* is shown in Fig. 3.2 (parameter estimates of the non-linear regression are shown in Appendix C1). There appeared to be two distinct phases: a rapid increase followed by a steady state of water content. In the initial phase, there was a rapid increase in water content from complete dehydration. The moss shoots rapidly surpassed more than 100% of its dry weight with only a very small amount of water (8 μL). This initial phase was characterized by vertical water conduction from the bottom to the tip of the shoot, followed by capillary movement along the leaves as described in the previous section. The second phase began at the inflection point in the curve where water content was around 30 μL. This phase appeared to be a steady-state that is characterized by reaching the maximum capacity for water content and a homogeneous distribution of water along the stem and leaves. Hydration culminated with no additional absorption and maximum water-holding capacity (300-1,000% of dry weight).

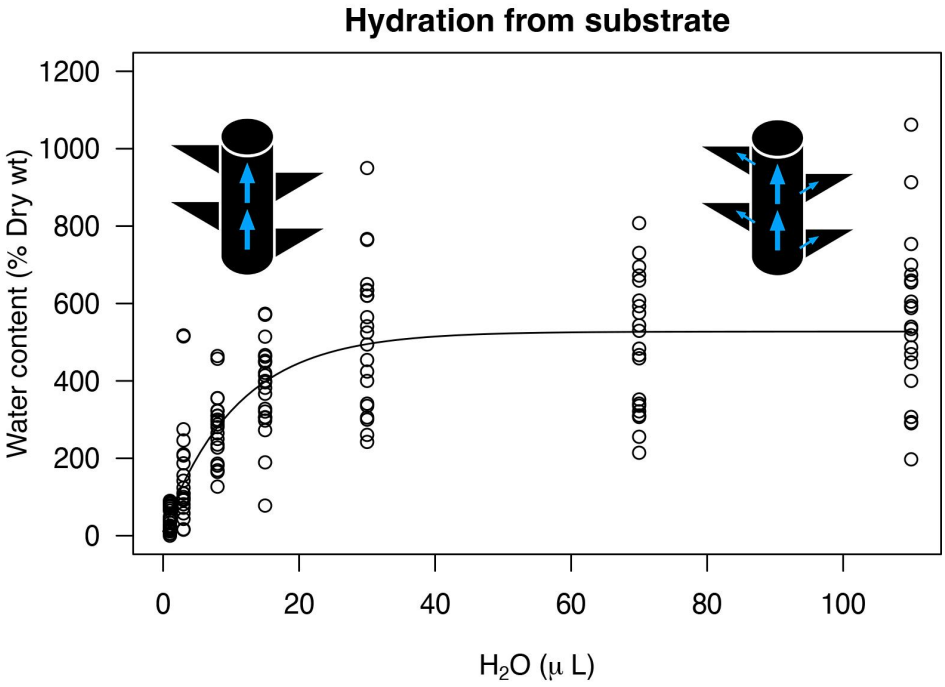

Figure 3.2. The curve of water content of a moss stem of six *Syntrichia* species (*S. campestris*, *S. calcicola*, *S. caninervis*, *S. papillosissima*, *S. ruralis*, and *S. squarripila*) depending on the amount of water applied to the base of the moss shoot.

Speed of conduction and holding capacity — The water holding capacity and speed of external conduction differed significantly among species of *Syntrichia* (Kruskal-Wallis test, p=1.7e-8, and p=4.1e-9, respectively) (Fig. 3.3). The water holding capacity showed nearly the opposite trend as the speed of external conduction. For instance, *S. amphidiaceae* (1,867% dry wt) and *S. papillosa* (1,804% dry wt) had higher water content at full turgor (Fig. 3.3, A), however, the lowest speed of external water conduction (0.06 mm/s and 0.0.4 mm/s, respectively) (Fig. 3.3, B). In contrast, *S. papillosissima* (391% dry wt), *S. calcicola* (366.8% dry wt.) and *S. caninervis* (349% dry wt) showed significantly similar low water holding capacity (p>0.72 for all three mean comparison) but high speeds of conduction. *S. caninervis* (0.37 mm/s) *and S. papillosissima* (0.34 mm/s) had significantly higher speeds of external transport (p=0.0001) than *S. calcicola* (0.19 mm/s) (Fig. 3.3, B). *S. bartramii* and *S. chisosa* had intermediate mean values of holding capacity (956 and 565.1 % dry wt, respectively) and speed of external conduction (0.13 and 0.11 mm/s, respectively). They only differed significantly in their water content at full turgor (p=0.001).

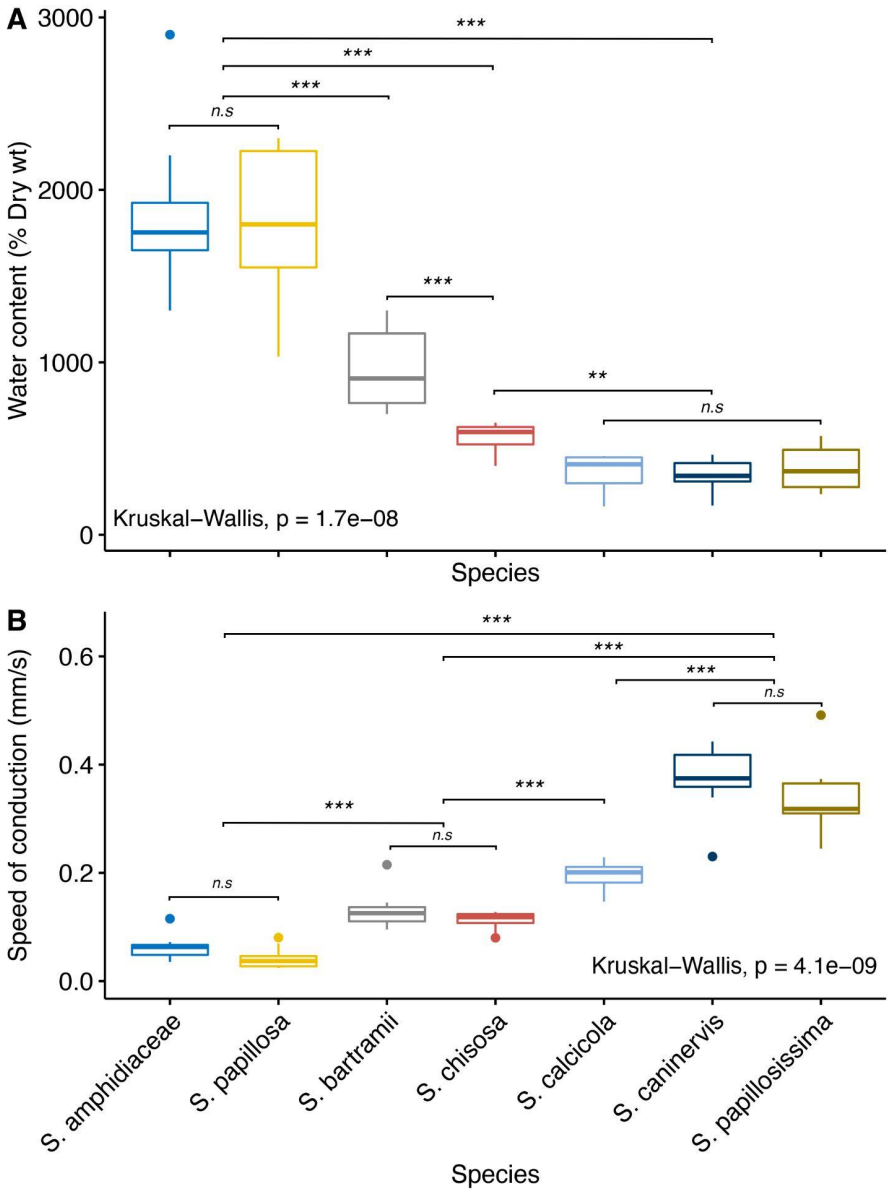

Figure 3.3. Water content (% of dry weight) (A) and speed of external (mm/s) (B) water conduction among different species of *Syntrichia*.

Dehydration curves — Dehydration curves showed a decrease in water content through time. We fitted the three curves using an asymptotic non-linear regression model (parameter estimates of the non-linear regression are shown in Supplementary Information Table S1). The three clumps differed in rate of dehydration as shown in Fig. 3.4. The densest clump (Clump 1) experienced a gradual decrease in water content, while the less dense clumps had a drastic decrease in water content. The denser clumps (Clump 1 and Clump 2) held a layer of water that remained significantly longer than in the clump that consisted of scattered stems (Clump 3) (Fig. 3.4, at the

right). The least dense clump (Clump 3) was almost completely dried after 10h while the other clumps dried after 25h.

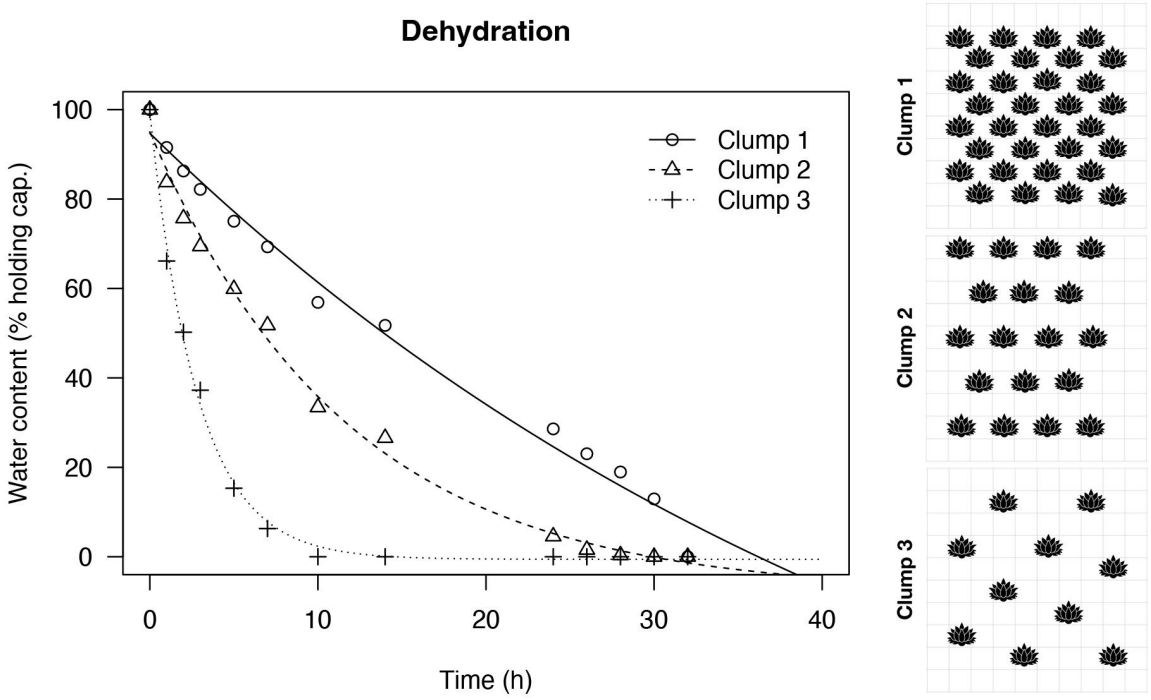

Figure 3.4. Dehydration curve of three clumps of *Syntrichia calcicola* with a different density of shoots. Clump 1 is a dense clump, similar to a clump growing in nature; Clump 2 is a modified clump with ~50% of the shoots of Clump 1; Clump 3 is a less dense clump with 25% of shoots of Clump 1.

Discussion

Structure and function of the external capillary system in Syntrichia — Based on these results, we propose a new integrated framework for understanding the link between morphology and water relationships in *Syntrichia*, which includes three morphological scales (Fig. 3.5). At the finest scale, leaf anatomy has three main characteristics that can be related to water uptake, conduction, and storage. At a larger scale, the individual stem possesses both hydrated and dehydrated architecture that influences the water relations. Finally, the proximity of each stem largely influences the clump's water capabilities (e.g., holding water capacity) in a given environment.

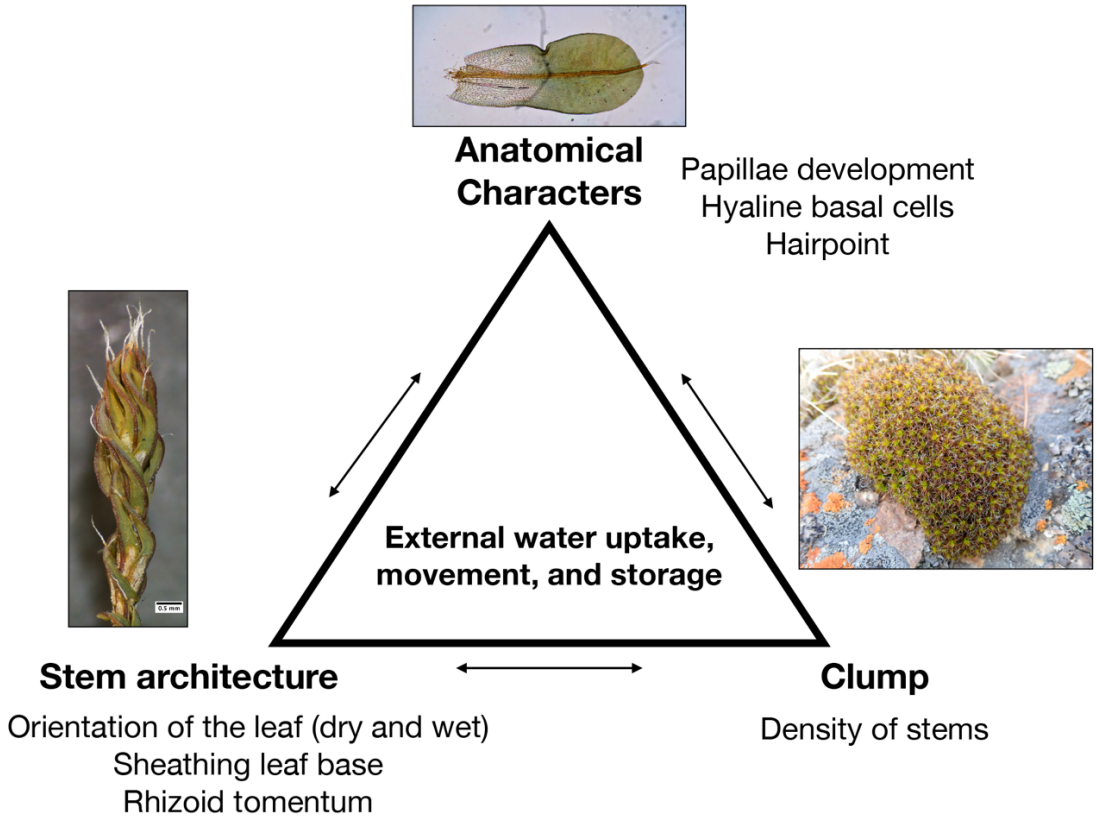

Figure 3.5. An integrated model for external water uptake, movement, and storage using as an example the dryland moss *Syntrichia*. The anatomical characters (e.g., papillae), stem architecture (e.g., sheathing bases), and the clump are three interconnected fundamental aspects of mosses that influence water relations.

The traits related to this external water conduction process vary among the species of *Syntrichia* studied here. The hyaline basal cells, ornamentation of papillae, and the hairpoint, represent crucial anatomical characteristics that influence water relations at a fine scale. Microscopic observations made here with a scanning electron microscope of leaves of *Syntrichia* showed that the hyaline basal cells are dead, hollow, and in some cases have perforated surfaces (Fig. 3.1). We suggest that these cells function in the refilling of water throughout the stem, acting

as a vertical pathway for fast uptake. For instance, they are likely actively involved in phase 1 of the hydration curve. These cells varied strongly across the species studied. *Syntrichia bartramii* has a low proportion of hyaline basal cells compared to the large, elongated, and extended proportion of the hyaline basal cells observed in *S. papillosissima* and *S. princeps*. Jauregui-Lazo et al., (in prep.) suggested that hyaline basal cells varied across the phylogeny of *Syntrichia*, and potentially this variation was associated with different strategies for absorbing and conducting water.

The mamillae and papillae of *Syntrichia* are distinct characters, often varying independently (Mishler, 1987). *Syntrichia* presents hollow papillae that could develop into three types of ornamentation: single (i.e., *S. papillosa)*, which consist of a single pointed projection; standard branching (i.e., *S. ruralis*), which has numerous small projections per cell but forked once; and antleroid branching (i.e., *S. papillosissima*), that consist of a single large projection but forked more than once in development. Despite the distinction in the ornamentation of papillae in *Syntrichia*, most of them created small capillary spaces (Proctor, 1982; Proctor et al., 1998). Here we demonstrated based on ESEM images that this network of capillary spaces can canalize water and move homogeneously across the leaf lamina, corroborating previous hypotheses and observations in *Syntrichia ruralis* (Proctor, 1982; Pressel and Duckett, 2011) and *S. intermedia* (Dilks and Proctor, 1979).

The microscopic observations of the hairpoint suggested that this character can be smooth or spinulose in the species studied. The hairpoint captures small drops of water from the atmosphere (Supplementary Video 4). Pan et al., (2016) also pointed out that the architecture of the hairpoint is important for water relations in *S. caninervis*. The grooves from the projections in a spinulose hairpoint, like *S. caninervis*, are able to form nano drops of free water. As the drops of water expand, they can be conducted towards the lamina and become available to the moss (Pan et al., 2016). Moreover, Tao and Zhang (2012), showed that the presence of the hairpoint influenced water relations in the moss *Syntrichia* by increasing water content and delaying evaporation rates.

The individual stem has a wide range of morphologies depending upon the level of hydration. There is a striking difference in mosses between leaf arrangement when dehydrated or hydrated, as illustrated herein by *Syntrichia* (Fig. 3.6). When dry, leaf orientation (whether crisped, twisted, keeled, or imbricated) may affect initial water uptake. For example, the combination of being keeled and twisted increases the total number of spaces available to distribute water along the ventral surface of the lamina. Whereas when the leaf is hydrated, the new leaf angle and shape may function in water-holding capacity (Wu et al., 2014). For example, *S. caninervis* spreads its leaves rapidly from an imbricate to a squarrose arrangement after rewetting to increase water storage and light capture (Wu et al., 2014). Presumably, the change in volume is mostly in leaf lamina since laminar cells are able to shrink completely when dry (Proctor et al., 1998) while hyaline cells remain intact. As hyaline basal cells sheathe the stem, and are perforated, they can provide an efficient external conducting system up the stem. The individual stem might act as a columnar pipe armed with the overlapping sheathing bases of leaves for water to be conducted efficiently. Supplementary Information Video 5-6 shows the stages of hydration and dehydration of several stems of *S. calcicola* and *S. caninervis*, respectively.

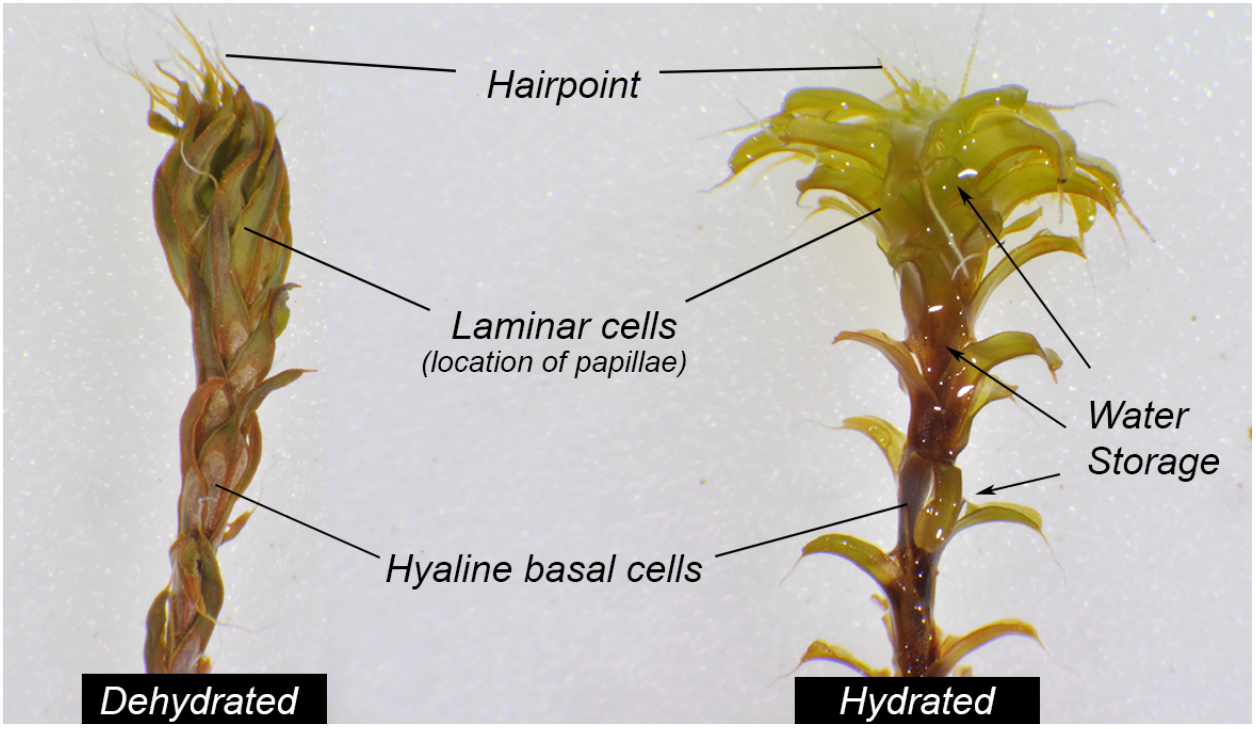

Figure 3.6. Two extremes of a morphological hydration spectrum in the moss *S. papillosissima*. Note the morphological differences between a fully dehydrated and hydrated stem.

The organization of the *Syntrichia* clump in nature is of variable density and while most species in *Syntrichia* can hold and transport water externally to some extent, a hydration event is influenced by the density of a clump. In this study, we showed that high densities of stems (Clump 1 and 2) hold water for longer than low densities (Clump 3). In addition to the fine capillary system in each stem, water is shared by adjacent stems within the clump forming an additional level in the capillary system.

Variation in morphological and anatomical characteristics might be at least partly associated with habitat preferences in *Syntrichia*. Epiphytic forms in *Syntrichia* vary in morphology compared to terricolous counterparts as shown in Chapter 2 (Jauregui et al., in prep.) This chapter showed that on average, epiphytic plants (*S. amphidiaceae* and *S. papillosa*) held almost twice as much water (1,835% Dry wt) as saxicolous plants (760% Dry wt) (*S. chisosa* and *S. bartramii*) and more than four times than terricolous species (369% Dry wt) (*S. calcicola, S. caninervis,* and *S. papillosissima*). Previous studies have reported similar values in water content in *Tortula intermedia* (*S. intermedia*) (Dilks and Proctor, 1979) and *T. ruralis* (*S. ruralis*) (Proctor *et al.*, 1998). The terricolous species had a higher speed of external water transport (0.302 mm/s) than either epiphytic (0.053 mm/s) or saxicolous (0.121 mm/s) species. *S. caninervis* had a significantly higher speed of external transport than other soil-dwelling species, such as *S. papillosissima* and *S. calcicola*. However, there was no difference either between *S. papillosa* and *S. amphidiaceae* (epiphytic species) ($p=0.10$) or *S. chisosa* and *S. bartramii* (saxicolous species) ($p=0.32$) species since they have very similar responses to external conduction.

There may be a trade-off between speed of conduction, and water holding capacity at full turgor, potentially associated with habitat preferences. Zotz (2016) suggested that a conglomerate

of traits (rather than a single one) makes a plant epiphytic. Plants of *Syntrichia* inhabiting trees are commonly bulbiform, have short hairpoint (or none), and a reduced proportion of basal hyaline cells that may or may not be perforated. But some species such as *S. amphidiacea* and S. *bartramii* can inhabit rocks and trees, and there is no clear pattern regarding *Syntrichia* habitat preferences and water relations. Future studies comprising a larger set of species need to be conducted, in a phylogenetic context, to address potential adaptive relationships between habitats, water relations, and plant morphology.

The ontogeny of the moss gametophyte might also contribute to the explanation of different responses to hydration and dehydration in relation to morphology. A distinct heteroblastic series occurs as a stem matures in *Syntrichia* (Mishler and Luna, 1991). Different types of leaves are produced depending on the ontogenic stage of the shoot. For instance, the base of the shoot is characterized by juvenile leaves that have no clear distinction of basal and laminar cells, and no hairpoint, while the upper part of the shoot consists of mature leaves with a clear distinction between basal and laminar cells, and a hairpoint (Mishler, 1986). As an acrocarpous moss, new shoots develop as new growth just below where the original shoot forms archegonia/antheridia at its tip. Thus, the heteroblastic series culminates in archegonia or antheridia. Therefore, if a species relies on asexual reproduction instead of sexual reproduction, as many epiphytic *Syntrichia* do, they may evolve to become neotenic and stop their development at a juvenile stage (Mishler, 1986). Many epiphytes have short, condensed stems bearing a juvenile form of leaves, i.e., short or no hairpoint, flat leaf lamina, and a short proportion of hyaline basal cells. These morphological traits do not capture, absorb, and or conduct water efficiently, but do retain water well. Further studies need to address potential evolutionary tradeoffs caused by the heteroblastic development between asexual reproduction and juvenile morphology compared to sexual reproduction and mature morphology.

External conducting systems in other mosses — Capillary conducting systems are diverse across mosses. The development of the papillae could be characterized by the number of projections per cell, presence of lumen, and ornamentation (i.e., branching type) (Câmara and Kellog, 2010; Glime, 2007). For example, a common type is a bifurcated individual projection (e.g., *Triquetrella*) (Malcolm and Malcolm, 2006). Examples of papillae are found in many unrelated groups of acrocarps, such as *Encalypta* (Encalyptaceae)*, Pleurochaete, Syntrichia, Triquetrella* (Pottiaceae), and *Orthotrichum* (Orthotrichaceae) (Proctor, 1979; Castaldo-Cobianchi and Giordano, 1984), and pleurocarps (e.g., Thuidiaceae, Theliaceae, Leskeaceae, Sematophyllaceae) (Hedenäs, 2001; Câmara and Kellog, 2010). Despite the diversity of organization of papillae, most create an interconnected network of channels ranging from 2 to 10 µm (Proctor, 1979; Proctor, 1982; Pressel and Duckett, 2011). Proctor (1982) developed a mathematical formulation indicating the rates of water movement for different capillary systems. The interspaces between papillae could create such a small tension (<150 kpa) to sustain extraordinary long-distance water transport (Proctor, 2011).

The diffusion of CO_2 is about 10,000 times slower in water than in air, thus external water conduction creates a potential problem for bryophytes (Dilks and Proctor, 1979). Indeed, net photosynthesis showed a decrease at extraordinary levels of water content (1,000- 1,500% of dry weight; Dilks and Proctor 1979; Green et al., 2011). Papillae may thus also function in gas exchange, by allowing higher CO_2 exchange when water is distributed across the lamina (Proctor, 1979). Fig. 3.2 shows how the water is distributed along the leaf surface in *Syntrichia* while some apices of the papillae remain uncovered and stand high among the channels filled with water as

suggested by Dilks and Proctor (1979). Supplementary Information Video 2-3 shows how lucifer yellow dye reacts with the apices of the papillae in *Syntrichia* because these areas could be hydrophobic in the rewetting phase. Proctor (1979, 2009) suggested that plants with squarrose or spreading leaves (and a concave shape) have a water-repellent lower surface and/or papillae for efficient gas exchange while the upper surface remain saturated (Green et al., 2011). This may represent an example of a "division of labor", in which one side of the leaf is specialized for water storage, while the other side is for gas exchange. This strategy has been shown in many mosses with an appressed leaf arrangement when dry, such as *Barbula sp.* (Rundel and Lange, 1980), *Weymouthia sp*., *Pleurozium,* and *Scleropodium* (Proctor, 2008).

At this time, a general understanding of the function of papillae is not possible given the great diversity of their structure and development. However, the capillary spaces among them are consistent across taxa and they potentially serve in part as an efficient pathway to move water from one place to another as demonstrated in *Syntrichia*. Future research needs to characterize the epidermal surface of the papillae from the base to the tip to know whether differentiation of the cuticle or wax thickness exists. For instance, a difference in wax thickness from the base to the bottom of the papillae would indicate a differential hydrophobic response of the papillae.

The most well-known example of external water relationships in mosses comes from *Sphagnum* (Mozingo et al., 1979). *Sphagnum* has two types of leaf cells which contribute to an unusual system for water storage and normal growth. One type is the typical chlorophyllous cells that perform photosynthesis, while the other type, the hyaline cells, are adjacent to the chlorophyllose cells and serve as water storage (Glime, 2007). Hyaline cells are clear because of a lack of chlorophyll or other pigments (Malcolm and Malcolm, 2006). The hyaline cells are dead but have a large perforation and spiral fibrils for additional strength (Hébant, 1977). Proctor (1979) found some similarities between the capillary system found in *Sphagnum* and the leaves of Pottiaceae and Calymperaceae, where the basal portion of mature leaves have elongated and thin-walled cells that are often perforated. Thus, there are similarities of the hyaline perforated cells between *Syntrichia* and *Sphagnum*, however, their function might be distinct. Since the hyaline basal cells of *Syntrichia* exist in a separate part of the leaf, sheath the stem (similar to the sheathing base of a grass leaf), and are perforated, they can provide an efficient external conducting system up the stem, acting as a vertical pathway for fast uptake, rather than functioning in water storing as seen in *Sphagnum* (Hájek and Beckett, 2008).

One of the most remarkable traits of mosses, which has received much attention, is the hairpoint. This morphological feature is often observed in mosses living in dry habitats and makes the moss look frosty in appearance. The hairpoint might function in several ways. Pan et al., (2016) demonstrated that hairpoint are able to capture small nanodrops of water from the atmosphere and conduct them toward the lamina in *S. caninervis* and suggested this may be an adaptation in mosses living in xerophytic environments. In addition, the hairpoint may function to minimize water loss by reflecting the sunlight and creating a boundary layer (Scott, 1982; Tao and Zhang, 2012). Conversely, the hairpoint may function to repel water when the amount of water is not sufficient to wet the plants fully and thus, they would be damaged by breaking dormancy without being able to recover. Whether the hairpoints or papillae are an adaptation to dry habitats, as suggested by Pan et al., (2016) and Castaldo-Cobianchi and Giordano (1984), respectively, requires additional pieces of evidence, especially an evolutionary framework. Deciding which traits are adaptations in a strict sense is a complicated inference process involving phylogenetics in addition to functional studies (Mishler, 1988; Brandon, 1990). A match between structure and function is not enough. To be an adaptation in a fundamental sense, the question is whether the trait evolved in

response to the particular environmental challenge that is hypothesized to have caused it. If the trait evolved before its current ecological function (and thus could not have been caused by that function) it is instead an *exaptation* (Gould and Vrba, 1982).

Leaf arrangement along the stem is also an important character of plant architecture that influences both photosynthesis and water use (van Zanten et al., 2010). Buch (1945) suggested that the spaces among leaves, such as the spaces among overlapping sheathing bases and the stem, can form a type of macro capillary system. In addition to the leaf arrangement, the rhizoidal tomentum on the stem may also provide capillary spaces to store and conduct water toward the tip of the stem in many mosses such as Dicranales and Bryales (Pressel and Duckett, 2011). Differences in stem anatomy between *Pleurozium schberia* and *Hylocomium splendens* revealed a distinct pathway for internal water conduction via apoplastic and symplastic transport using fluorescent tracers (Sokolowska et al., 2017). In vascular plants, the angle of leaf insertion determines water storage capacity and stem water flow (Garcia-Estringana et al., 2010), which may be similar in hydrated mosses. In comparison with vascular plants, we would emphasize the importance of the leaf arrangement in both a dry and wet stage because they each influence water relations at different times.

Clump structure (growth form) is noticeably different across various mosses and causes differing interactions with water (Sand-Jensen and Hammer, 2012). Clump structure is quite important for water absorption and retention (Rice and Schneider, 2004). For example, *Grimmia pulvinata* grows as a cushion at different sizes. A larger cushion has a thicker boundary layer and a lower surface-to-volume ratio that confers lower evaporation rates (Zotz et al., 2000). Clump structure influences air flow near the boundary layer; thus, the roughness of the canopy is critical to increasing or decreasing evaporation rates (water flux) (Rice et al., 2001). In general, greater roughness of a cushion tends to create turbulent air flow near the moss reducing the boundary layer and increasing evaporation rates (Rice and Schneider, 2004). However, mosses tend to grow compactly in dry habitats, thus reducing drying rates and holding water by adjacent shoots within the canopy to form an integrated capillary network (Nakatsubo, 1994; Rice and Schneider, 2004).

The response to hydration of a whole clump will be different than a single stem by itself, or of a leaf by itself. Indeed, the effect of individual shoot morphology on water properties may be marginal as compared to the clump structure. The density of the clump as a whole determined the drying rate in a study of subarctic bryophytes (Elumeeva et al., 2011). After heavy rain, the moss clump achieves full turgor as the excess of water drains away (Proctor, 2011), and a dense clump maximizes water retention.

Future work needed on the relationship of ectohydry to ecology and evolution — As discussed in the introduction, all land plants inherited some plesiomorphic characters from their freshwater algal ancestors, such as a moderate level of desiccation tolerance. But various land plant lineages developed different traits, both physiological and morphological, for dealing with water scarcity in different land environments, i.e., some lineages evolved internal water conduction, while others relied on external water conduction.

Ectohydry is a complex phenomenon where multiple factors of morphology play a role in space and time. In a recent survey, Patiño et al., (2022) highlighted that the functions of morphological features, such as hairpoints, paraphyllia, and paraphyses, in relation to fitness and physiological performance still remain open as one of 50 fundamental questions in bryology. Here we suggest a conceptual strategy to analyzing the external water relationships of mosses in an integrated manner (Fig 7). Future studies are needed to survey traits relating to external water

conduction more widely among mosses. In addition, the evolution of environmental preferences needs to be studied in more detail. Once this additional information is available, phylogenetic comparative methods should be applied to determine the evolutionary origins of structural traits in relation to the environment present at that time. In this way, adaptive changes in evolution can be discovered.

Data availability statement

The Supplementary Information related to the video recordings is available at Dryad upon request: https://datadryad.org/stash/share/kMcfezUpXvd4tqBus-Aodh1TAXEmSrX8QjT9YLwD9WI. Supplementary Video 1: External water movement along an individual stem showing some important morphological characters for external water movement and storage (the hyaline basal cells, keeled leaves, papillae, recurvature of leaf margin) when free water is applied from the base in *S. papillosissima*. Supplementary Video 2: 3-D reconstruction of papillae in *S. bartramii* using LYCH as a dye in confocal microscopy. Supplementary Video 3: 3-D reconstruction of papillae in *S. papillosissima* using LYCH as a dye in confocal microscopy. Supplementary Video 4: Hydration of the clump when spraying small drops of water in *S. calcicola*. Supplementary Video 5: Hydration and dehydration of a clump when free water is applied from the base in *S. calcicola*. Supplementary Video 6: Hydration and dehydration of a clump when free water is applied from the base in *S. caninervis*.

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Appendices

Appendix A. Supplementary files for Chapter 1.

Appendix A1. Voucher information for the specimens used in this study. Taxon names (family, species, and author), taxon names used on the tree (OTU), and GENBANK accession (ITS, rcbL, trnL-F, and rps4) for each species.

Family	**Species**	**OTU**	**ITS**	**rbcL**	**trnL-F**	**rps4**
Amblystegiaceae	*Campylium polygamum* (Schimp.) Lange & C.E.O. Jensen	*C. stellatum*	AY663362.1		AY663347.1	HE717067.1
Amblystegiaceae	*Cratoneuropsis chilensis* (Lorentz) Ochyra		MN179598.1		MN239144.1	MN239157.1
Amblystegiaceae	*Vittia pachyloma* (Mont.) Ochyra				AY242384.1	AY908240.1
Amphidiaceae	*Amphidium tortuosum* (Hornsch.) Cufod.		KY175151.1		KY175109.1	
Andreaeaceae	*Andreaea alpina* Hedw.	*A. rothii*		1:AF231060.1 2:AY608025.1	AY608120.1	AF306952.1
Andreaeaceae	*Andreaea subulata* Harv.			1: JN388785.1 2: JN388784.1		
Andreaeobryaceae	*Andreaeobryum macrosporum* Steere & B.M. Murray	*Outgroup*		AF231059.1		AF306953.1
Anomodontaceae	*Chileobryon callicostelloides* (Broth. ex Thér.) Enroth		FM161088.1		FM210283.1	FM882222.1
Aulacomniaceae	*Hymenodontopsis mnioides* (Hook.) N.E. Bell, A.E. Newton & D. Quandt	*Pyrrhobryum mnioides*		AY854002.1	AY143047.1	AY142971.1
Bartramiaceae	*Bartramia ithyphylloides* Schimp. ex Müll. Hal.		HF536685	AY151188		AF491045.1
Bartramiaceae	*Bartramia patens* Brid.		MK948546.1		MK948581.1	1:MK948574.1 2:MN010593.1
Bartramiaceae	*Bartramia stricta* Brid.		HF536696.1		AY651834.1	AF023799.1
Bartramiaceae	*Breutelia integrifolia* (Taylor) A. Jaeger		MN179596.1		MN239143.1	MN239156.1
Bartramiaceae	*Philonotis esquelensis* Matteri	*P.thwaitesii*		AF491019.1	AF497132.1	
Bartramiaceae	*Philonotis krausei* (Müll. Hal.) Broth.	*P. falcata*	KC111046.1	AY151184.1	AF497114.1	AF491048.1
Bartramiaceae	*Philonotis minuta* (Taylor) A. Jaeger	*P. vescoana*			AF497124.1	AF491046.1
Bartramiaceae	*Philonotis polymorpha* (Müll. Hal.) Kindb.	*P. fontana*	KC111071.1	AY631192.1	AF497121.1	AF491031.1
Bartramiaceae	*Philonotis scabrifolia* (Hook. f. & Wilson) Braithw.			AY151186.1	AF497116.1	AF491042.1
Bartramiaceae	*Philonotis vagans* (Hook. f. & Wilson) Mitt.			AF491007.1	AF497131.1	

Brachytheciaceae	*Rhynchostegium acanthophyllum* (Mont.) A. Jaeger	*E. acanthophylla*	DQ336904.1		DQ336927.1	AY908299.1
Bryaceae	*Anomobryum julaceum* (Schrad. ex G. Gaertn., B. Mey. & Scherb.) Schimp.			AJ275172.1	KX355917.1	KX355951.1
Bryaceae	*Bryum algovicum* Sendtn. ex Müll. Hal.				AY150346.1	AF521678.1
Bryaceae	*Bryum argenteum* Hedw.		MK234276.1	LC270450.1; AY163024.1	EF362488.1	MK234319.1
Bryaceae	*Bryum bicolor* Dicks.		EU878214.1	AY163025.1	AY150349.1	AF521681.1
Bryaceae	*Bryum billarderii* Schwägr.	*B. orthothecium*		AY163038.1	AY163156.1	AY163091.1
Bryaceae	*Bryum pseudotriquetrum* (Hedw.) G. Gaertn., B. Mey. & Scherb.		MK270310.1	AY163040.1	: AY150357.1	MK270328.1
Bryaceae	*Bryum sauteri* Bruch & Schimp.		EU878216.1		DQ539462.1	
Bryaceae	*Bryum torquescens* Bruch & Schimp.	*B. muehlenbeckii*			AY078310.1	AY078337.1
Bryaceae	*Bryum typeI*	*B. turbinatum*		KM408767.1	KX355928.1	1: KX355960.1 2: JF277334.1
Bryaceae	*Bryum typeII*	*B. caespiticium*		AF478245.1	EF362491.1	AF478281.1
Bryaceae	*Bryum typeIII*	*B. coronatum*	EU878212.1	AY163031.1	DQ539451.1	AY163090.1
Bryaceae	*Bryum typeIV*	*B. clavatum*		AY163030.1	AY163153.1	
Bryaceae	*Bryum typeV*	*B. gemmiferum*		AY163035.1	DQ539455.1	AY163089.1
Bryaceae	*Bryum valparaisense* Thér.	*B. schleicheri*			JF277367.1	JF277333.1
Bryaceae	*Bryum viridescens* Welw. & Duby	*B. pallens*			AY150356.1	AF521688.1
Bryaceae	*Rosulabryum campylothecium* (Taylor) J.R. Spence	*R. capillare*	AJ252136.1	LC270446.1	LC270620.1	LC270533.1
Calliergonaceae	*Warnstorfia exannulata* (Schimp.) Loeske		DQ400061.1		DQ404993.1 DQ404994.1	AY907968.1
Calliergonaceae	*Warnstorfia fluitans* (Hedw.) Loeske				KM363586.1	
Catagoniaceae	*Catagonium nitens* (Brid.) Cardot		GU568688.1	DQ463108.1	AF472449.1	
Chrysoblastellaceae	*Chrysoblastella chilensis* (Mont.) Reimers			AB914714.1		AB914713.1
Cryphaeaceae	*Dendrocryphaea cuspidata* (Sull.) Broth.					AY908587.1
Daltoniaceae	*Achrophyllum magellanicum* (Besch.) Matteri		HQ613477.1		HQ613674.	HQ613599

Dicranellaceae	*Dicranella hookeri* (Müll. Hal.) Cardot	*D. cerviculata*	KM594586.1	MK353895.1	AF129597.1	1: MN187485.1 2:MN187486.1
Dicranellaceae	*Dicranella campylophylla* (Taylor) A. Jaeger	*D. heteromalla*	KM594587.1	AF231296.1		1: MN187499.1 2: AF231272.1
Ditrichaceae	*Ceratodon purpureus* (Hedw.) Brid.		AY156592.1	2: DQ463103.1; 3: EU095321.1	AF435310.1	AJ554004.1
Ditrichaceae	*Ditrichum conicum* (Mont.) Mitt.	*D. flexicaule*	MN179600.1	AF231301.1	DQ397194.1	AF231278.1
Ditrichaceae	*Ditrichum difficile* (Duby) M. Fleisch.	*D. heteromallum*		MH595721.1		LC176263.1
Fissidentaceae	*Fissidens curvatus* Hornsch.	*F. taxifolius*	KC333220.1	LC272008.1		LC272062.1; DQ463123.1
Fissidentaceae	*Fissidens rigidulus* Hook. f. & Wilson	*F. fontanus*		LC271976.1		LC272030.1
Funariaceae	*Funaria chilensis* (Thér.) Thér.	*F. microstoma*	JN089175.1		JN088949.1	JN088981.1
Funariaceae	*Funaria hygrometrica* Hedw.		JN089174.1		JN088948.1	JN088980.1
Grimmiaceae	*Dryptodon trichophyllus* (Grev.) Brid.		KX443522.1		AJ879777.1	DQ399624.1
Grimmiaceae	*Grimmia laevigata* (Brid.) Brid.		EU343776.1	AF231081.1	JQ936849.1	AF478283.1
Grimmiaceae	*Grimmia pseudoanodon* Deguchi	*G. anodon*	EU343758.1	GU808970.1	JQ936856.1	JQ936876.1
Grimmiaceae	*Grimmia reflexidens* Müll. Hal.		EU343791.1			KX024331.1
Grimmiaceae	*Racomitrium lamprocarpum* (Müll. Hal.) A. Jaeger	*Bucklandiella lamprocarpa*	HE584706.1			
Grimmiaceae	*Schistidium andinum* (Mitt.) Herzog		MG582285.1			
Grimmiaceae	*Schistidium scabripes* (E.B. Bartram) Deguchi	*S. apocarpum*		GU808984.1		AY908145.1
Lembophyllaceae	*Looseria orbiculata* (Thér.) D. Quandt, Huttunen, Tangney & M. Stech		AF509860.1		AF509563.1	
Lembophyllaceae	*Rigodium brachypodium* (Müll. Hal.) Paris	*R. implexum*	FM161209.1		AF543547.1	MG199033.1
Lembophyllaceae	*Rigodium toxarion* (Schwägr.) A. Jaeger		AF509843.2	GQ497670.1	AF509546.1	1: AY908331.1;2: MG199007.1
Leucobryaceae	*Campylopus incrassatus* Kunze ex Müll. Hal.		KU163125.1		KU212887.1	
Leucobryaceae	*Campylopus introflexus* (Hedw.) Brid.		AY925208.1		KY619018.1	AY908128.1
Leucobryaceae	*Campylopus pyriformis* (Schultz) Brid.		AY551406.1;			
Leucobryaceae	*Campylopus vesticaulis* Mitt.	*C. pilifer*	GU446694.1		AY542534.1	

Mniaceae	*Pohlia cruda* (Hedw.) Lindb.			MG733067.1	LC270403.1	JF277360.1	JF277325.1
Mniaceae	*Pohlia nutans* (Hedw.) Lindb.			AF479319.1	1: LC270425.1; 2: AY631193.1	JF277353.1; KX355935.1	JF277319.1; JF277318.1
Mniaceae	*Pohlia wahlenbergii* (F. Weber & D. Mohr) A.L. Andrews				LC270439.1	LC270613.1; LC270612.1	1:LC270526.1; 2:LC270525.1
Neckeraceae	*Leptodon smithii* (Dicks. ex Hedw.) F. Weber & D. Mohr			FM161147.1	GQ497667.1	JF690818.1; HQ381074.1	AY908261.1
Orthotrichaceae	*Orthotrichum rupestre* Schleich. ex Schwägr.			KT804256.1		MH175977.1	MH175861.1
Polytrichaceae	*Oligotrichum canaliculatum* (Hook. & Arn.) Mitt.				AY118242.1	AF545013.1	AY137687.1
Polytrichaceae	*Polytrichum juniperinum* Hedw.			MF180458.1	AY118262.1	MF180575.1; MF180574.1	AY137705.1
Pottiaceae	*Andina coquimbensis* (J.A. Jiménez & M.J. Cano) J.A. Jiménez & M.J. Cano					JN968427.1	
Pottiaceae	*Bryoerythrophyllum recurvirostrum* (Hedw.) P.C. Chen			KU058177.1		GU953731.1	KY406861.1
Pottiaceae	*Didymodon andreaeoides*	Cardot & Broth.	*D. torquatus*	MF536563.1			MF536613.1
Pottiaceae	*Didymodon australasiae* (Hook. & Grev.) R.H. Zander			MN683500.1		KX176741.1	MN696670.1
Pottiaceae	*Didymodon fuscus* (Müll. Hal.) J.A. Jiménez & M.J. Cano			KP307467.1			KP307537.1
Pottiaceae	*Didymodon santessonii* (E.B. Bartram) J.A. Jiménez & M.J. Cano		*D. rigidulus*	AY854391.1	KM408771.1	AY950401.1; KX176740.1	HM147768.1
Pottiaceae	*Didymodon tophaceus* (Brid.) Lisa			MF536579.1		JN968449.1	MF536612.1
Pottiaceae	*Didymodon vinealis* (Brid.) R.H. Zander			KP307469.1	KM408772.1	JN968450.1;GU 953729.1	EU274593.1
Pottiaceae	*Gymnostomum calcareum* Nees & Hornsch.			MN817242.1		KX176744.1	MN815940.1
Pottiaceae	*Hennediella heimii* (Hedw.) R.H. Zander			JX679956.1		KF418162.1;	JX679980.1:
Pottiaceae	*Hennediella kunzeana* (Müll. Hal.) R.H. Zander			GQ339752.	S514	S514	S514
Pottiaceae	*Pseudocrossidium carinatum* (Gillies ex Grev.) R.H. Zander					KR677400.1; KR677399.1	
Pottiaceae	*Pseudocrossidium chilense* R.S. Williams		*P. replicatum*		Villalobos_sn_Jan2008	GU953717.1; Villalobos_sn_Jan2008	unknown|MX_Tlaxcala
Pottiaceae	*Pseudocrossidium crinitum* (Schultz) R.H. Zander					KR677409.1; KR677408.1	
Pottiaceae	*Pseudocrossidium leucocalyx* (Mont.) Thér.		*P. denticulatum*			KR677413.1; KR677411.1	MF536623.1

Pottiaceae	*Pseudocrossidium perpapillosum* M.J. Cano & J.A. Jiménez	*P.revolutum*	JX679942.1		JN968452.1	JQ890482.1
Pottiaceae	*Pseudocrossidium santiagense* (Broth.) M.J. Cano				KR677418.1	
Pottiaceae	*Sagenotortula quitoensis* (Taylor) R.H. Zander		GQ339761.1	S424	S424	
Pottiaceae	*Syntrichia breviseta* (Mont.) M.J. Cano & M.T. Gallego			S_366	S_366	S_366
Pottiaceae	*Syntrichia campestris* (Dusén) R.H. Zander			S_368	S_368	S_368
Pottiaceae	*Syntrichia epilosa* (Broth. ex Dusén) R.H. Zander			S_544	S_544	S_544
Pottiaceae	*Syntrichia glacialis* (Kunze ex Müll. Hal.) R.H. Zander	*S. anderssonii*		S_362		S_362
Pottiaceae	*Syntrichia lithophila* (Dusén) Ochyra & R.H. Zander			S_381	S_562	S_381
Pottiaceae	*Syntrichia muricata* M.T. Gallego & M.J. Cano			S_565	S_565	S_565
Pottiaceae	*Syntrichia pseudorobusta* (Dusén) R.H. Zander			S_567	S_567	
Pottiaceae	*Syntrichia robusta* (Hook. & Grev.) R.H. Zander			S_392	S_574	S_392
Pottiaceae	*Syntrichia scabrella* (Dusén) R.H. Zander			S_579	S_579	S_579
Pottiaceae	*Syntrichia scabrinervis* (Müll. Hal.) R.H. Zander			S_591	S_591	S_591
Pottiaceae	*Syntrichia serripungens* (Lorentz & Müll. Hal.) R.H. Zander			S_595	S_595	S_595
Pottiaceae	*Syntrichia squarripila* (Thér.) Herzog	*S. antarctica*		S_525	S_364	S_364
Pottiaceae	*Tortula hoppeana* (Schultz) Ochyra	*T. bolanderi*	JN544710.1	S_410	S_410	S_410
Pottiaceae	*Tortula jaffuelii* Thér.	*T. inermis*	AY934553.1	S_432	S_432	1:AF480993.1 2:MUB_7900
Pottiaceae	*Triquetrella patagonica* Müll. Hal.				1:AM491746.1 2:AM491745.1	1:AM491752.1 2:AM491751.1
Pottiaceae	*Weissia controversa* Hedw.			LC183770.1	KT380333.1	AF480976.1
Rhabdoweisiaceae	*Camptodontium cryptodon* (Mont.) Reimers				1:MN718479.1 2:MN718478.1	1:MN718540.1 2:MN718539.1
Rhabdoweisiaceae	*Symblepharis krausei* (Lorentz) Ochyra & Matteri	*S. vaginata*		MH595726.1	1:MN092435.1; 2:AF435349.1	MN092569.1
Scorpidiaceae	*Sanionia uncinata* (Hedw.) Loeske		FJ572355.1	FJ572302.1	1: HQ452034.1 2: HQ452033.1	FJ572608.1
Seligeriaceae	*Blindia contecta* (Hook. f. & Wilson) Müll. Hal.	*B. acuta*	KX387349.1	AF226817.1	KX387230.1	AF023781.1

Sematophyllaceae	*Rhaphidorrhynchium callidum* (Mont.) Broth.	*R. amoenum*	KX278711.1	KX130415.1	KU950799.1	KU936463.1
Sphagnaceae	*Sphagnum magellanicum* Brid.	*Outgroup*	AY298533.1	MF362295.1	AY298167.1	MF362441.1
Stereophyllaceae	*Catagoniopsis berteroana* (Mont.) Broth.					AY908200.1
Stereophyllaceae	*Juratzkaea seminervis* (Kunze ex Schwägr.) Lorentz	*J. sinenis*	KF770684.1		KF770522.1	KF770576.1
Takakiaceae	*Takakia lepidozioides* S. Hatt. & Inoue J.	*Outgroup*		AY312936.1	AY312947.1	AF306950.1

Appendix B. Supplementary files for Chapter 2.

Appendix B1. Voucher information for the specimens used in this study. Name used on tree (species name on packet), species name, location of the collection (country and geographic area), herbarium identification (collector, collection number, and herbarium information), and SRA accession number.

Name used on tree	**Species name**	**Location**	**Herbarium ID**	**SRA accession**
Barbula_unguiculata_Ke1050	*Barbula unguiculata* Hedw.	US_California	Kellman_1050_UC	SRR19887030
Chenia_leptophylla_No104926	*Chenia leptophylla* (Müll. Hal.) R.H. Zander	Iran	Norris_104926_UC	SRR19887029
Dolotortula_mniifolia_Li490	*Dolotortula mniifolia* (Sull.) R.H. Zander	Bolivia	Linneo_490_MO	SRR19887018
Hennediella_antarctica_S_513	*Hennediella antarctica* (Ångstr.) Ochyra & Matteri	CL_XII	Brinda_5373_UC	SRR19887007
Hennediella_stanfordensis_Sh19275	*Hennediella stanfordensis* (Steere) Blockeel	US_California	Shevock_19275_UC	SRR19886996
Leptodontium_capituligerum_De6772	*Leptodontium capituligerum* Müll. Hal.	MX_Mexico	Delgadillo_6772_UC	SRR19886985
Leptodontium_pungens_De1996	*Leptodontium pungens* (Mitt.) Kindb.	MX_Mexico	Delgadillo_1996_UC	SRR19886974
Sagenotortula_quitoensis_S_409	*Sagenotortula quitoensis* (Taylor) R.H. Zander	Bolivia	Lewis_38581_MO	SRR19886963
Saitobryum_lorentzii_Su610	*Saitobryum lorentzii* (Müll. Hal.) Ochyra	Argentina	Suarez_610_MO	SRR19886952
Streblotrichum_convolutum_S_406	*Streblotrichum convolutum* (Hedw.) P. Beauv.	US_California	Shevock_19360_CAS	SRR19886941
Streptopogon_erythrodontus_No92595	*Streptopogon erythrodontus* (Taylor) Wilson ex Mitt.	Ecuador	Norris_92595_UC	SRR19887028
Syntrichia_aculeata_S_361	*Syntrichia aculeata* (Wilson) Spruce	Bolivia	Lewis_87786_UC	SRR19887027
Syntrichia_ammonsiana_S_001	*Syntrichia ammonsiana* (H.A. Crum & L.E. Anderson) Ochyra	US_West_Virginia	Brinda_9596_MO	SRR19887026
Syntrichia_amphidiaceae_S_005	*Syntrichia amphidiacea* (Müll. Hal.) R.H. Zander	US_North_Carolina	Brinda_8680_UC	SRR19887025
Syntrichia_andersonii_S_362	*Syntrichia anderssonii* (Ångstr.) R.H. Zander	CL_XII	Brinda_5253_UC	SRR19887023

Syntrichia_anderssonii_S_398	*Syntrichia anderssonii* (Ångstr.) R.H. Zander	CL_XII	Larrain_39392_MO	SRR19887024
Syntrichia_andicola_S_010	*Syntrichia andicola* (Mont.) Ochyra	MX_Mexico	Vitt_17509_UC	SRR19887022
Syntrichia_angustifolia_S_363	*Syntrichia angustifolia* (Herzog) M.J. Cano	Bolivia	Lewis_87764_UC	SRR19887021
Syntrichia_antarctica_S_364	*Syntrichia antarctica* (Hampe ex Müll. Hal.) R.H. Zander	CL_XII	Brinda_5501_UC	SRR19887020
Syntrichia_austroafricana_S_365	*Syntrichia austroafricana* (W. A. Kramer) R.H. Zander	South_Africa	Magill_5905_MO	SRR19887019
Syntrichia_bartramii_S_019	*Syntrichia bartramii* (Steere) R.H. Zander	US_Texas	Brinda_8182_UC	SRR19887017
Syntrichia_bogotensis_S_022	*Syntrichia bogotensis* (Hampe) R.H. Zander	MX_Mexico	Cardenas_4375_UC	SRR19887016
Syntrichia_breviseta_S_366	*Syntrichia breviseta* (Mont.) M.J. Cano & M.T. Gallego	CL_RM	Jauregui_270_UC	SRR19887015
Syntrichia_buchtienii_S_367	*Syntrichia buchtienii* (Herzog) M.J. Cano & M.T. Gallego	CL_III	Ibanez_sn_09_03_2017_MO	SRR19887014
Syntrichia_buchtienii_S_416	*Syntrichia buchtienii* (Herzog) M.J. Cano & M.T. Gallego	CL_II	Mahu_08626_MO	SRR19887013
Syntrichia_cainii_S_026	*Syntrichia cainii* (H.A. Crum & L.E. Anderson) R.H. Zander	CA_Ontario	Buck_56584_CAS	SRR19887012
Syntrichia_calcicola_S_033	*Syntrichia calcicola* J.J. Amann	Iran	Norris_104694_UC	SRR19887011
Syntrichia_campestris_S_368	*Syntrichia campestris* (Dusén) R.H. Zander	CL_RM	Jauregui_471_UC	SRR19887010
Syntrichia_caninervis_S_043	*Syntrichia caninervis* Mitt.	US_Idaho	Brinda_9434_UC	SRR19887009
Syntrichia_cavallii_S_369	*Syntrichia cavallii* (G. Negri) Ochyra	Ethiopia	G_and_S_Miehe_1458a_MO	SRR19887008
Syntrichia_chisosa_S_077	*Syntrichia chisosa* (Magill, Delgad. & L.R. Stark) R.H. Zander	US_New_Mexico	Brinda_2539a_MO	SRR19887006
Syntrichia_christophei_S_371	*Syntrichia christophei* Ochyra & R.H. Zander	CL_XII	Larrain_39470_MO	SRR19887005
Syntrichia_conferta_S_370	*Syntrichia conferta* (E.B. Bartram) R.H. Zander	Antarctica	Bernardo_239_MO	SRR19887004
Syntrichia_costesii_S_372	*Syntrichia costesii* (Thér.) R.H. Zander	CL_RM	Jauregui_469_UC	SRR19887003
Syntrichia_echinata_S_082	*Syntrichia echinata* (Schiffn.) Herrnst. & Ben-Sasson	US_California	Kellman_4202_CAS	SRR19887002
Syntrichia_epilosa_La42483A	*Syntrichia epilosa* (Broth. ex Dusén) R.H. Zander	CL_VII	Larrain_42483A_MO	SRR19887001
Syntrichia_filaris_S_373	*Syntrichia filaris* (Müll. Hal.) R.H. Zander	Antarctica	Ochyra_5251_79_MO	SRR19887000
Syntrichia_flagellaris_S_374	*Syntrichiadelphus flagellaris* (Schimp.) Brinda, Jáuregui-Lazo & Mishler	CL_V	Jauregui_66_UC	SRR19886999
Syntrichia_fragilis_S_085	*Syntrichia fragilis* (Taylor) Ochyra	US_Arizona	Brinda_2092_UC	SRR19886998
Syntrichia_geheeebiaeopsis_S_375	*Syntrichia geheebiaeopsis* (Müll. Hal.) R.H. Zander	CL_XII	Brinda_5244_UC	SRR19886997
Syntrichia_gemmascens_S_376	*Syntrichia gemmascens* (P.C. Chen) R.H. Zander var. gemmascens	China	Shevock_49194_CAS	SRR19886995

Syntrichia_glacialis_S_377	*Syntrichia glacialis* (Kunze ex Müll. Hal.) Spruce	CL_XI	Larrain_27093_MO	SRR19886994
Syntrichia_handelii_S_092	*Syntrichia handelii* (Schiffn.) S. Agnew & Vondr.	Greece	Cano_sn_26-VII-1999_MO	SRR19886993
Syntrichia_intermedia_S_221	*Syntrichia intermedia* Brid.	Iran	Norris_104517_UC	SRR19886992
Syntrichia_kingii_S_094	*Syntrichia kingii* (H. Rob.) M.T. Gallego & M.J. Cano	MX_Queretaro	Delgadillo_6660_CAS	SRR19886991
Syntrichia_lacerifolia_S_379	*Syntrichia lacerifolia* (R.S. Williams) R.H. Zander	Bolivia	Churchill_and_Serrano_23411_MO	SRR19886990
Syntrichia_laevipila_S_098	*Syntrichia laevipila* Brid.	US_California	Hillyard_and_Norris_106797_UC	SRR19886989
Syntrichia_latifolia_S_118	*Syntrichia latifolia* (Bruch ex Hartm.) Huebener	US_California	Norris_and_Hillyard_109731_UC	SRR19886988
Syntrichia_leucostega_S_380	*Syntrichia leucostega* (Müll. Hal.) R.H. Zander	South_Africa	Hedderson_14998_MO	SRR19886987
Syntrichia_lithophila_S_381	*Syntrichia lithophila* (Dusén) Ochyra & R.H. Zander	CL_XII	Larrain_38465_CAS	SRR19886986
Syntrichia_longimucronata_S_382	*Syntrichia longimucronata* (X.J. Li) R.H. Zander	China	Shevock_27376_CAS	SRR19886984
Syntrichia_magellanica_S_383	*Syntrichia magellanica* (Mont.) R.H. Zander	CL_XII	Brinda_5232_UC	SRR19886982
Syntrichia_magellanica_Och4884	*Syntrichia magellanica* (Mont.) R.H. Zander	Antarctica	Ochyra_4884/79_UC	SRR19886983
Syntrichia_magilliana_S_384	*Syntrichia magilliana* L.E. Anderson	South_Africa	Bester_5863_MO	SRR19886981
Syntrichia_minor_S_118	*Syntrichia minor* (Bizot) M.T. Gallego, J. Guerra, M.J. Cano, Ros & Sánchez-Moya	US_California	Norris_55341_UC	SRR19886980
Syntrichia_montana_S_122	*Syntrichia montana* Nees.	France	Brinda_11051_UC	SRR19886979
Syntrichia_muricata_JJ1035A	*Syntrichia muricata* M.T. Gallego & M.J. Cano	CL_IV	Jauregui_1035A_UC	SRR19886978
Syntrichia_napoana_S_385	*Syntrichia napoana* (De Not.) M.J. Cano & M.T. Gallego	Ecuador	Norris_91126_UC	SRR19886977
Syntrichia_norrisii_S_147	*Syntrichia* cf. *virescens* (De Not.) Ochyra.	US_California	Ahart_11497_UC	SRR19886976
Syntrichia_norvegica_S_167	*Syntrichia norvegica* F. Weber	US_Washington	Brinda_9237_UC	SRR19886975
Syntrichia_obtussisima_S_178	*Syntrichia obtusissima* (Müll. Hal.) R.H. Zander	MX_Mexico	Delgadillo_6060_UC	SRR19886973
Syntrichia_pagorum_S_184	*Syntrichia pagorum* (Milde) J.J. Amann	US_Arizona	Brinda_2211_UC	SRR19886972
Syntrichia_papillosa_S_193	*Syntrichia papillosa* (Wilson ex Spruce) Spruce	US_Missouri	Brinda_7142_UC	SRR19886971
Syntrichia_papillosissima_S_201	*Syntrichia papillosissima* (Copp.) Loeske	US_Arizona	Brinda_2209_UC	SRR19886970
Syntrichia_percarnosa_S_218	*Syntrichia percarnosa* (Müll. Hal.) R.H. Zander	Bolivia	Linneo_337-A_MO	SRR19886969
Syntrichia_phaea_S_386	*Syntrichia phaea* (Hook. f. & Wilson) R.H. Zander	New_Zealand	Allen_3950_MO	SRR19886968
Syntrichia_princeps_S_225	*Syntrichia princeps* (De Not.) Mitt. var. princeps	US_California	Brinda_8400_UC	SRR19886967
Syntrichia_prostrata_S_387	*Syntrichia prostrata* (Mont.) R.H. Zander	CL_VIII	Ireland_and_Bellolio_35273_CAS	SRR19886966
Syntrichia_pseudohandelii_S_389	*Syntrichia pseudohandelii* (J. Froehl.) S. Agnew & Vondr.	Iran	Norris_104518_UC	SRR19886965

Syntrichia_pseudorobusta_S_388	*Syntrichia pseudorobusta* (Dusén) R.H. Zander	CL_XVI	Ireland_and_Bellolio_35943_CAS	SRR19886964
Syntrichia_ramosissima_S_390	*Syntrichia ramosissima* (Thér.) R.H. Zander	CL_RM	Jauregui_293_UC	SRR19886962
Syntrichia_rigescens_S_391	*Syntrichia rigescens* (Broth. & Geh.) Ochyra	Iran	Norris_104541_UC	SRR19886961
Syntrichia_robusta_S_392	*Syntrichia robusta* (Hook. & Grev.) R.H. Zander var. robusta	CL_XII	Brinda_5305_UC	SRR19886960
Syntrichia_rubella_S_393	*Syntrichia rubella* (Hook. f. & Wilson) R.H. Zander	Australia	Streimann_6151_MO	SRR19886959
Syntrichia_rubra_S_394	*Syntrichia rubra* (Mitt.) R.H. Zander	Australia	Streimann_53607_MO	SRR19886958
Syntrichia_ruraliformis_S_395	*Syntrichia ruraliformis* (Besch.) Mans.	Germany	Abts_6000_CAS	SRR19886957
Syntrichia_ruralis_B_9108	*Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr	CA_Alberta	Brinda_9108_MO	SRR19886956
Syntrichia_saxicola_S_577	*Syntrichia saxicola* (Cardot) R.H. Zander	CL_XII	Larrain_33119_MO	SRR19886955
Syntrichia_scabrella_S_397	*Syntrichia scabrella* (Dusén) R.H. Zander	CL_RM	Jauregui_182_UC	SRR19886954
Syntrichia_scabrinervis_S_399	*Syntrichia scabrinervis* (Müll. Hal.) R.H. Zander	CL_RM	Jauregui_294_UC	SRR19886953
Syntrichia_serrata_S_400	*Syntrichia serrata* (Dixon) R.H. Zander	Australia	Streimann_59750_MO	SRR19886951
Syntrichia_serripungens_S_401	*Syntrichia serripungens* (Lorentz & Müll. Hal.) R.H. Zander	Bolivia	Churchill_24663_MO	SRR19886950
Syntrichia_serrulata_S_402	*Syntrichia serrulata* (Hook. & Grev.) M.J. Cano	CL_X	Larrain_25834_MO	SRR19886949
Syntrichia_sinensis_S_304	*Syntrichia sinensis* (Müll. Hal.) Ochyra	US_New_Mexico	Brinda_2607_UC	SRR19886948
Syntrichia_squarripila_S_403	*Syntrichia squarripila* (Thér.) Herzog ex Brinda, Jáuregui-Lazo & Mishler	CL_RM	Larrain_42093_MO	SRR19886947
Syntrichia_submontana_S_405	*Syntrichia submontana* (Broth.) Ochyra	Russia	Afonina_sn_26_Aug_2011_MO	SRR19886946
Syntrichia_subpapillosa_S_404	*Syntrichia subpapillosa* (Cardot & Broth.) Matteri	CL_XII	Brinda_5152_MO	SRR19886945
Syntrichia_subpapillosissima_S_307	*Syntrichia subpapillosissima* (Bizot & R.B. Pierrot ex W.A. Kramer) M.T. Gallego & J. Guerra	CA_Alberta	Brinda_9106_UC	SRR19886944
Syntrichia_sucrosa_S_366	*Syntrichia sucrosa* Kellman	US_California	Kellman_6137_CAS	SRR19886943
Syntrichia_virescens_S_337	*Syntrichia virescens* (De Not.) Ochyra	Iran	Mishler_3814_UC	SRR19886942
Tortula_inermis_Sh21585	*Tortula inermis* (Brid.) Mont	US_Nevada	Shevock_21585_UC	SRR19886940
Tortula_muralis_Sh29403	*Tortula muralis* Hedw.	US_California	Shevock_29403_UC	SRR19886939
Tortula_platyphylla_JJ259	*Tortula platyphylla* Mitt	CL_RM	Jauregui_259_UC	SRR19886938
Tortula_plinthobia_No105784	*Tortula plinthobia* (Sull. & Lesq.) Broth.	US_California	Norris_105784_UC	SRR19886937
Tortula_subulata_Sh29941	*Tortula subulata* Hedw.	US_California	Shevock_29941_UC	SRR19886936

Trichostomum_brachydontium_B8175	*Trichostomum brachydontium* Bruch	US_Texas	Brinda_8175_UC	SRR19886935
Willia_austroleucophaea_S_411	*Willia austroleucophaea* (Besch.) Broth.	CL_XII	Brinda_5108_UC	SRR19886934
Willia_brachychaete_S_608	*Willia brachychaete* (Dusén) R.H. Zander	CL_VII	Jauregui_507_UC	SRR19886933

Appendix B2. A detailed description of anatomical and morphological characters used for creating the morphological matrix (98 OTUs x 43 characters). Each character was coded for each specimen in the phylogeny.

Item	Character	Description	Character states
General characteristics	1. Flagellate stems	A whip-like stem	0=Present; 1=Absent.
	2. Hyalodermis	A crossed section of the stem showing a row of enlarged thin-walled cells around the stem.	0=Present; 1=Absent.
	3. Leaf orientation (dry)	Arrangement of leaves around the stem.	0= leaves individually crisped (strongly wavy); 1= leaves individually twisted (bread); 2= leaves twisted together around the stem, longitudinally infolded (rosette or bulbiform); 3= appressed or imbricate (e.g., *S. caninervis*); 4= leaves crisped in a rosette.
	4. Leaf keeled (dry)	Whether the leaves are keeled (folded) when they are dry.	0= keeled; 1= not keeled.
	5. Leaf stance (moist)	Plants soaked in warm water until full expansion.	0= leaves squarrose-recurved (blade and apex recurved, >90° respect to the stem); 1= spreading (blade between, 45° to 90°); 2: erect-patent (blade slightly recurved, <45°).
Leaf morphology	6. Leaf shape (widest point)	Overall shape of a mature leaf.	0= lanceolate (widest at base & tapering); 1= oblong (leaf margin parallel for at least 2/3 of leaf length); 2= spatulate (widest in upper half, *S. princeps*); 3= ovate (widest in lower part); 4= oblong but acute at tip; 5= rounded (e.g., *Saitobryum*)
	7. Leaf constriction in the middle (i.e., panduriform)	Any noticeable constriction of leaf width in the middle part of the leaf.	0= absent; 1= present.

	8. Leaf serration	Projections in the form of teeth on the margin.	0= entire; 1= irregularly toothed near apex; 2= short (unicellular) in lamina; 3= long (multicellular with a base) along the margin below the apex (e.g., *S. pseudorobusta*).
	9. Leaf margin	Whether the edge of the leaf has a degree of recurvature	0=erect to plane throughout; 1=reflexed; 2=recurved to revolute; 3= incurved.
	10. Leaf border	Presence of thicker, smoother cell walls, or double strata at the border.	0= leaves not bordered; 1= leaves bordered by a thicker wall; 2= presence of double strata.
	11. Laminal strata	Thickness of cross-section above the middle of the leaf.	0= unistratose; 1= bistratose patches; 2= uniformly bistratose or multistratose.
	12. Concavity of leaves	Whether the margin and leaf lamina curve inward or outward	0= carinate (folded along the middle with reverse curve along either side); 1= V-shaped (folded along the middle without reverse curvature); 2= flat; 3= notched.
Upper laminal cells	13. Upper leaf surface	Location of the papillae	0= papillose both sides; 1=papillae on one side; 2= smooth (no papillae).
	14. Development of papillae	A projection from a cell surface that is hollow and developed by successive bifurcations.	0= simple (e.g., *S. papillosa*); 1= standard branching (twice branched, e.g., *S. ruralis*); 2= antleroid branches (thicker & longer branches, e.g., *S. papillosissima*).
	15. Number of papillae	Number of papillae per cell.	0= multiple; 1= one (e.g., *S. papillosissima*).
	16. Development of mammillae	Cell surface bulging.	0= flat; 1= present; 2= extreme (e.g., more than 5 µm).
	17. Upper leaf cell size	Measure the length of the cell perpendicular to the leaf axis. Mean of 10 randomly selected upper medial cells per leaf.	0 = 5 to 10µm; 1 = 11 to 15µm; 2 = 15-20 µm; 3= >20 µm.
	18. Collenchymatous laminal cells	Cell walls more heavily thickened at the angles.	0= absent; 1= present.
	19. Shape of leaf apex	Shape of the protruding part of the leaf	0= acuminate; 1= acute; 2= obtuse; 3= emarginate; 4= cucullate.
Lower basal cells	20. Basal cell differentiation	Degree of the transition between the lower-smooth-hyaline cells and the papillose upper laminal cells.	0=no differentiation; 1= gradual differentiation; 2= abrupt differentiation; 3= U-shaped differentiation.
	21. Perforation of basal cells	Whether the basal cells are dead and hollow.	0= no hollow; 1=incipient hollow; 2= hollow.

	22.	Basal cell group ratio	As a proportion of the total length of the leaf.	0 = 1/5 of total length; 1 = 1/3 of total length; 2 = ½ of total length.
	23.	Sheathing leaf base	Whether the group of basal cells are sheathing (clasping) the stem.	0 = absent; 1 = present
	24.	Basal cell width	Mean of the width of 10 randomly selected cells from the basal group.	0 = 10 to 15 µm; 1 = 15 to 20 µm; 2 = >20 µm.
	25.	Basal cell length	Mean of the length of 10 randomly selected cells from the basal group.	0 = short (e.g., virescens); 1 = long (more variable).
	26.	Basal cells papillose	Presence of papillae in basal cells.	0 = absent; 1 = present.
Costa	27.	Shape of costa	Organization of the specialized cell in the midrib	0 = elliptic or crescent (e.g., *Leptodontium sp*.); 1 = rounded but fragile or few cells; 2 = rounded but robust with stereids (e.g., *Syntrichia sp*.).
	28.	Costa extension	Whether the costa extends beyond the tip of the blade.	0 = costa percurrent (present throughout the leaf, but not extending beyond lamina); 1= costa excurrent as mucro; 2 = costa excurrent as short awn (spine); 3 = costa excurrent as a hairpoint.
	29.	Serration of hairpoint	Presence of sharp teeth along the hairpoint	0 = absent; 1 = present
	30.	Costa papillose	Papillae along the dorsal side of costa (homologous to leaf papillae).	0 = absent; 1 = simple; 2 = branched (stellate).
	31.	Costa with prorae	Having projections formed by projecting cell ends.	0 = absent; 1 = present and short; 2 = present and long.
	32.	Guide cells	Presence of one or more medial cells	0= Small or undifferentiated; 1= Differentiated and large.
	33.	Subguide cells	Presence of cells with large lumens abaxial to guide cells.	0 = absent; 1 = presence.
	34.	Stereid band	Position of stereid band in the costa.	0= double band (dorsal and ventral); 1 = Only one band (dorsal)
	35.	Stereid cells	Number of rows of stereid cells (small lumens and thick colored walls)	0 = 1 to 2 (e.g., *S. virescens);* 1 = 3 to 5; 2 = more than 5.
	36.	Epidermal cell (abaxial):	A differentiated layer of cells on the abaxial surface of the costa.	0 = present; 1 = absent.

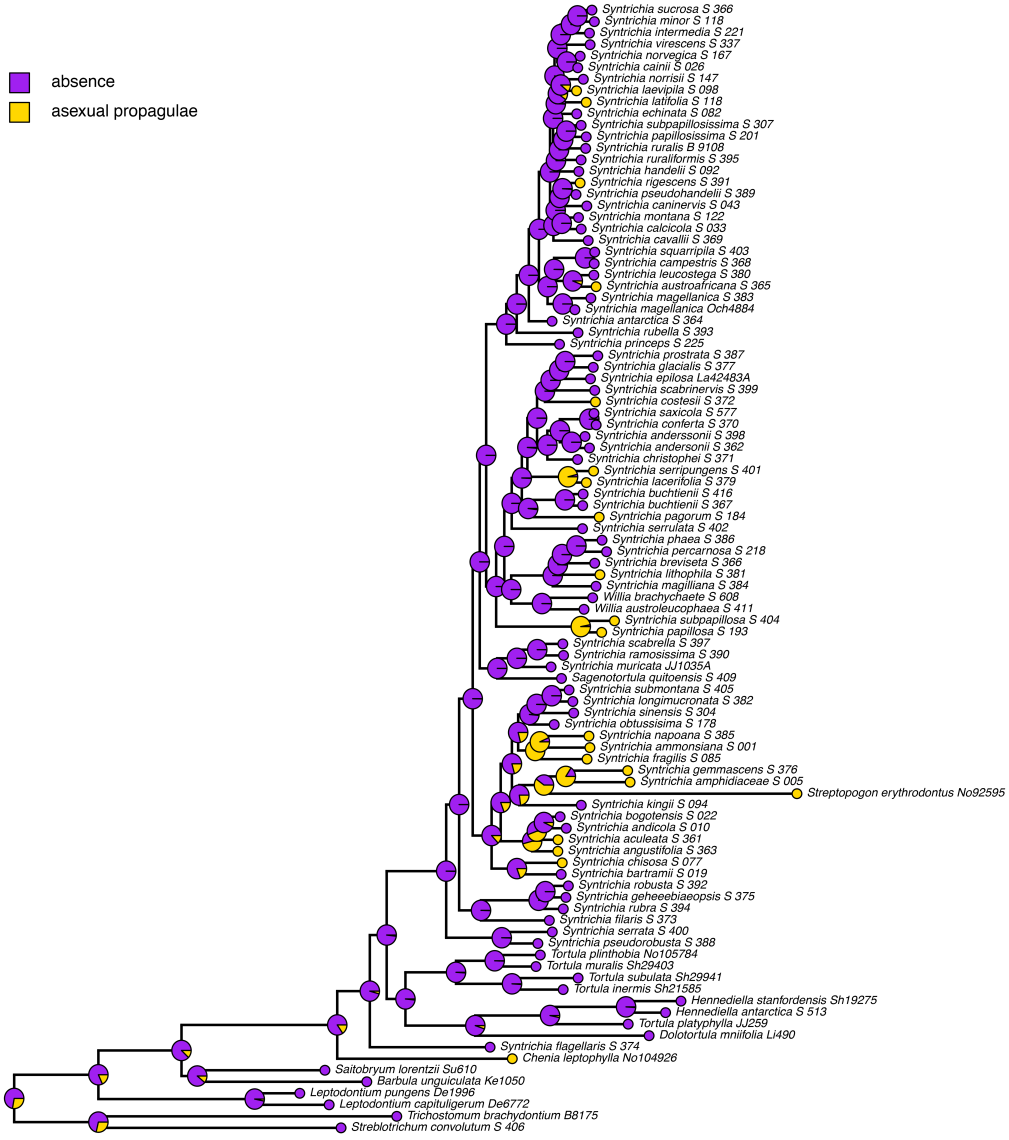
	37.	Epidermal cell (adaxial)	A layer of unicellular cells in the ventral (adaxial) side of the costa (excluding stereids cells).	0 = absent; 1 = present.
	38.	Hydroids	Any recognizable differentiation of hydroids.	0 = present; 1 = absent.
Reproduction	39.	Asexual	Specialized vegetative diaspores.	0 = absent; 1 = brood leaves; 2 = leaf-borne gemmae. 3 = axillary gemmae (modified axillary hairs); 4 = caducous leaf apex; 5 = fragile lamina.
	40.	Sexuality	Sexual reproduction.	0 = monoicous; 1 = dioicous.
	41.	Sexuality (part 2)	If monoicous,	0 = autoicous; 1 = paroicous; 2 = synoicous.
Sporophyte	42.	Peristome	Teeth surrounding the opening of the capsule.	0 = large (1/2 to 2/3 of total length; 1 = medium (1/3-1/2 of total length); 2 = small (<1/4); 3 = no peristome or rudimentary.
Chemical reaction	43.	KOH reaction	Colored cell wall after applying KOH.	0 = yellow; 1 = red.

Appendix B3. Comparison between morphological and molecular trees. A: Best ML tree from the morphological dataset with colored bootstrap branch support (1,000 bootstrap replicates). B: ML tree from probes regions with colored bootstrap branch support (1,000 bootstrap replicates). Blue text indicates the congruence of clades between both trees (partial congruence is indicated by *), while orange text indicates incongruencies between morphological and molecular datasets.

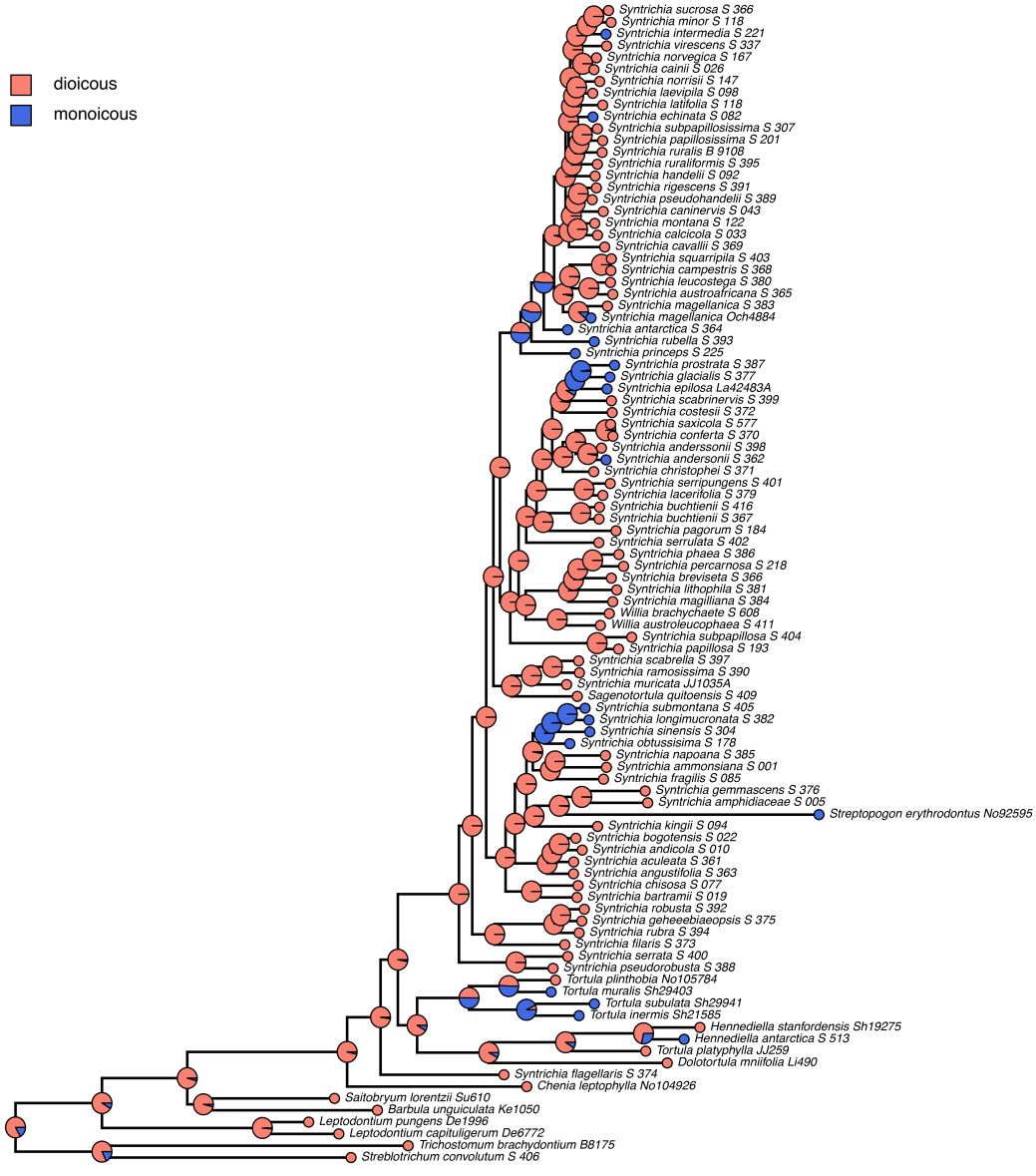
Appendix B4. LnL, AIC and AIC ratio statistics from BioGeoBEARS used to compare different biogeographic models.

Biogeographic model	LnL	p-value	AIC	AIC weight ratio model
DEC	-325.8	0.043	655.5	0.35
DEC+J	-323.7		653.4	2.86
DIVAlike	-331.6	1	667.2	2.72
DIVAlike+J	-331.6		669.2	0.37
BAYAREAlike	-295.3	1	594.6	2.72
BAYAREAlike+J	-295.3		596.6	0.37

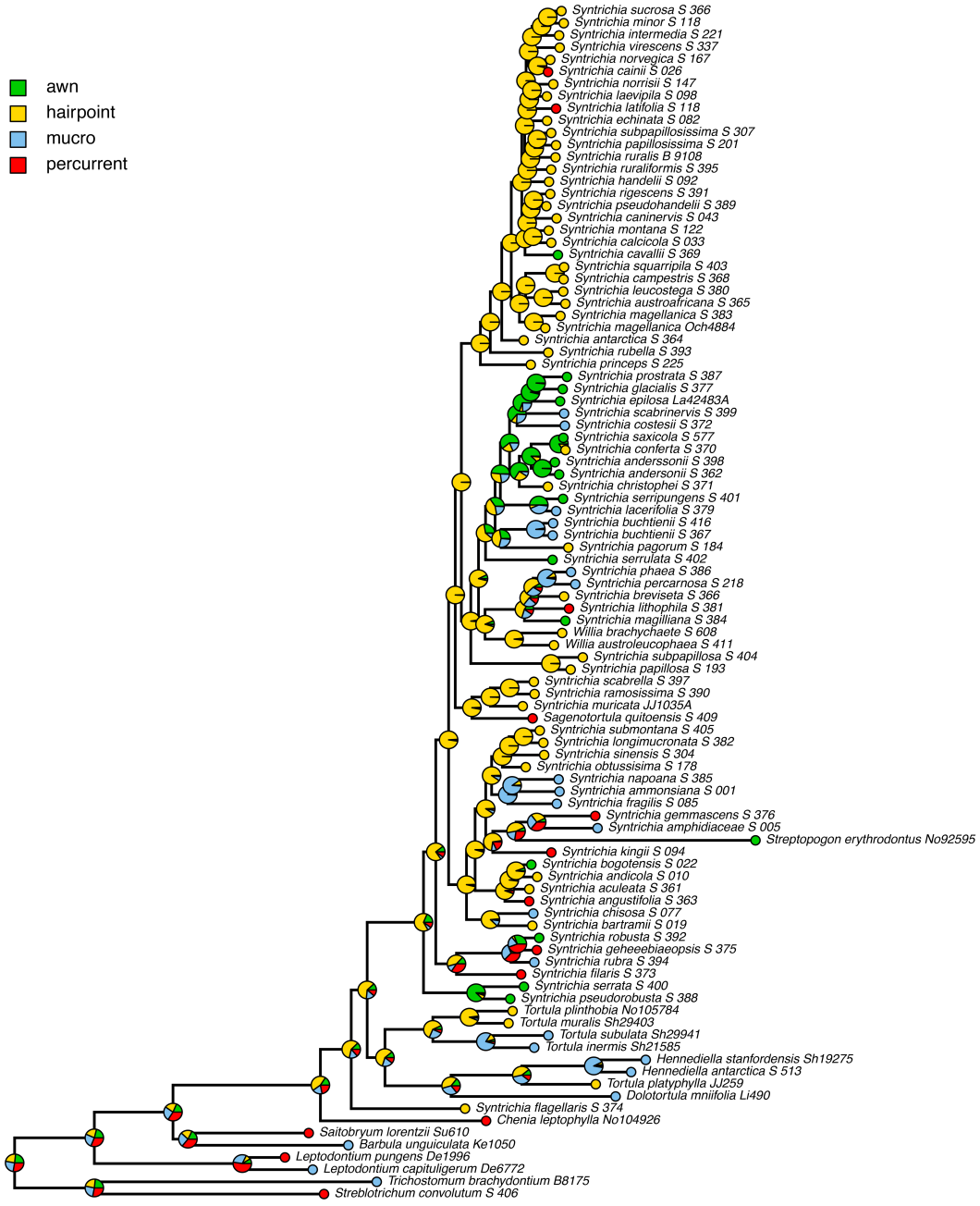
Appendix B5. Ancestral character reconstruction of a discrete trait (asexual reproduction) in *Syntrichia* using an ER model of evolution. States are the presence or absence of propagulae.



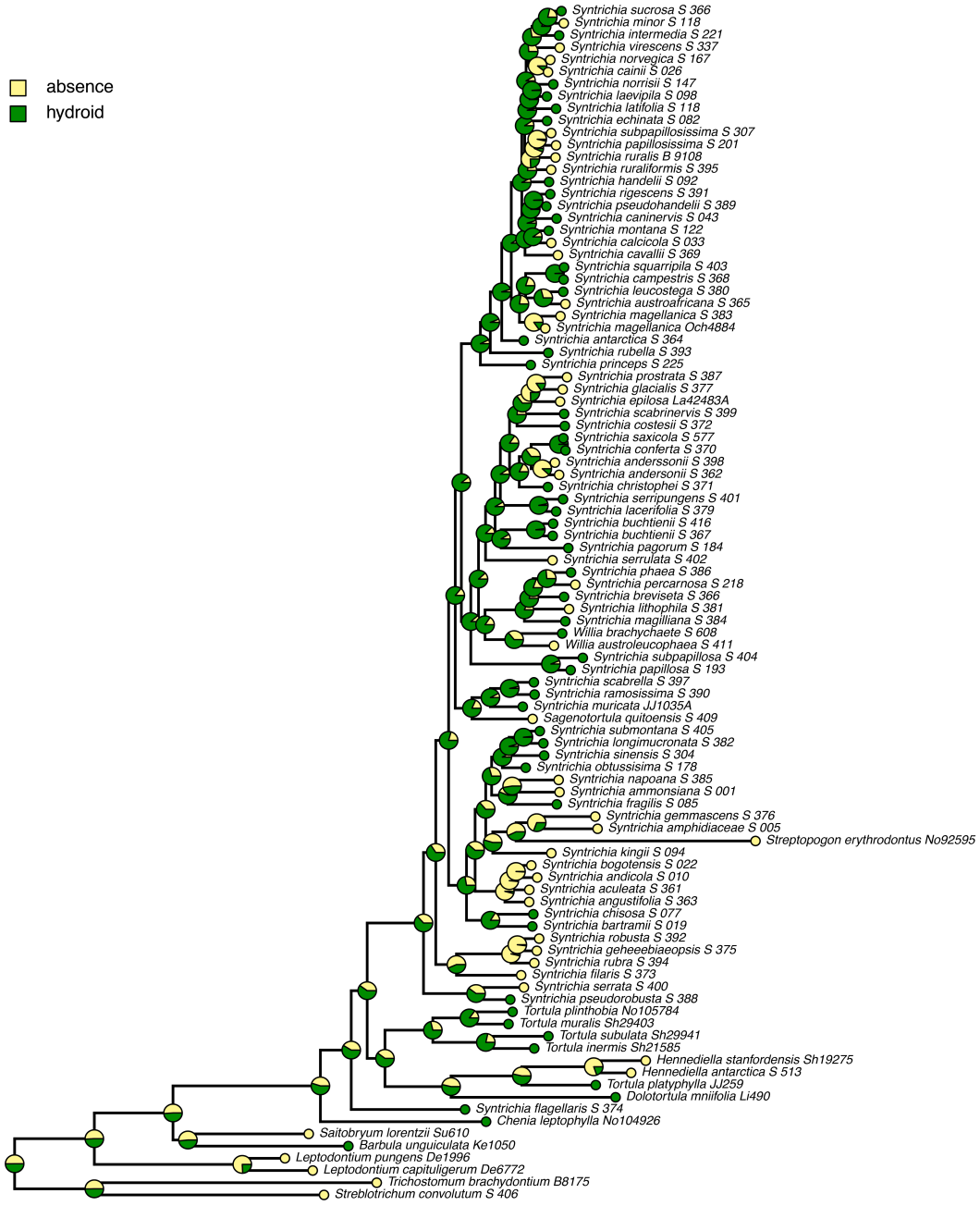
Appendix B6. Ancestral character reconstruction of a discrete trait (reproduction) in *Syntrichia* using an ER model of evolution. States are dioicous or monoicous.



Appendix B7. Ancestral character reconstruction of a discrete trait (extension of the costa) in *Syntrichia* using an ER model of evolution. States of the costa condition are percurrent, mucro, awn, and hairpoint.



Appendix B8. Ancestral character reconstruction of a discrete trait (hydroids in the costa) in *Syntrichia* using an ER model of evolution. States are presence and absence of hydroids.



Appendix C. Supplementary files for Chapter 3.

Appendix C1. Estimates of parameters for the non-linear regression used to estimate the hydration and dehydration curves. Signif. codes: 0 '***'; 0.001 '**'; 0.01 '*'.

Parameter estimates	Estimate Std.	Error	t-value	p-value
Hydration curve Model fitted: Asymptotic Regression Model (3 parms)				
init:(Intercept)	10.967697	33.794768	0.3245	0.746
m:(Intercept)	0.092343	0.016635	5.5513	1.325e-07 ***
plateau:(Intercept)	527.462221	21.099251	24.9991	< 2.2e-16 ***
Residual standard error: 146.1812 (144 degrees of freedom)				
Dehydration curve Model fitted: Asymptotic Regression Model (3 parms)				
init:Clump 1	94.7032652	1.4084107	67.2412	< 2.2e-16 ***
init:Clump 2	95.0060274	1.7038717	55.7589	< 2.2e-16 ***
init:Clump 3	99.1600982	2.2281553	44.5032	< 2.2e-16 ***
m:Clump 1	0.0200175	0.0054328	3.6846	0.000321 ***
m:Clump 2	0.0853876	0.0065364	13.0634	< 2.2e-16 ***
m:Clump 3	0.3531271	0.0178977	19.7303	< 2.2e-16 ***
plateau:Clump 1	-89.0387854	36.5513504	-2.4360	0.0160469 *
plateau:Clump 2	-8.0731995	2.5490655	-3.1671	0.0018725 **
plateau:Clump 3	-0.5766212	0.9606343	-0.6003	0.5492635
Residual standard error: 4.986599 (147 degrees of freedom)				