Widespread Infection of the Hair Lichen Genus *Bryoria* (Parmeliaceae) by a Previously Unknown Fungal Pathogen

by

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ABSTRACT

Bryoria Brodo & D. Hawksw. (Parmeliaceae, Ascomycota) is one of the dominant genera of hair lichens in western North America and is characteristic of high elevation conifer forest ecosystems. In areas where *Bryoria* is abundant, it is common to find thalli in which the thalline filaments become conglutinated, forming brittle dead zones, or "rattails". I sampled *Bryoria* thalli across western Canada and the northwestern United States monitoring thallus dieback at different times of the year. I found that this dieback phenomenon is associated with the winter growth of a mold-forming basidiomycete not previously known to associate with *Bryoria*. Similar *Bryoria* die-off has been attributed to extreme rain events in British Columbia and Norway, but not in the presence of a necrotrophic mold. I report that this fungus belongs to *Athelia* Pers., a cosmopolitan genus of the basidiomycete family Atheliaceae containing economically significant pathogens. To place the *Bryoria*-associated fungi within *Athelia*, I designed *Athelia*-specific primers for two gene regions (EF1-α and ITS) and screened the mold directly along with apparently uninfected lichen specimens to assess its potential latent occurrence. The pathogen initially appeared to be related to *A. epiphylla* Pers. and *A. acrospora* Jülich, a species heretofore known only from dead wood. Based on phylogenetic placement along with its distinctly sized basidia and basidiospores, this mold is presented here as *Athelia seborrheica,* a new species. It was found to frequently infect members of *Bryoria* sect. *Implexae* (Gyeln.) Brodo & D. Hawksw., occasionally associates with other foliose and fruticose species within Parmeliaceae, and does not appear to exist within thalli asymptomatically. Whether or not this widespread infection of *Bryoria* in western North America is a recent event or simply an overlooked

phenomenon is difficult to determine with certainty. This research will serve as a benchmark for documenting the pathogenic outbreak affecting an ecologically significant lichen genus.

PREFACE

This thesis is an original work by Spencer Goyette. Toby Spribille advised the methodology and approach, and Viacheslav Spirin (University of Helsinki) provided crucial specimens of *Athelia* as well as insight regarding that genus.

DEDICATION

But when you tread on this clutch of nettles
that was once me, reading this in some other century
like an outdated story, remember that I was innocent
and that like you, mortals of your day, I too
had a face marked by anger, and by pity, and by joy.

A man's face, quite simply.

Benjamin Fondane, "Préface en Prose", translated by John Balaban

One must have a mind of winter
To regard the frost and the boughs
Of the pine-trees crusted with snow;

And have been cold a long time
To behold the junipers shagged with ice,
The spruces rough in the distant glitter

Of the January sun; and not to think
Of any misery in the sound of the wind,
In the sound of a few leaves,

Which is the sound of the land
Full of the same wind
That is blowing in the same bare place

For the listener, who listens in the snow
And, nothing himself, beholds
Nothing that is not there and the nothing that is.

Wallace Stevens, "The Snow Man"

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CHAPTER 1

Widespread Infection of the Hair Lichen Genus *Bryoria* (Parmeliaceae) by a Previously Unknown Fungal Pathogen

1 INTRODUCTION

Sensitive to pollution and disturbance, the presence of lichens within a given habitat can be a useful indication of that habitat's health, age, and productivity (McCune, 2000). In boreal and montane forests, epiphytic lichens, such as those belonging to the genus *Bryoria* Brodo & D. Hawksw. (Parmeliaceae), interact with other organisms in a variety of ways. They serve as a crucial winter food source to sustain herds of critically endangered woodland caribou (Edwards et al., 1960; Rominger et al., 1996; Thomas et al., 1996; Johnson et al., 2000) and other ungulates (Ward & Marcum, 2010), are used as nesting material by flying squirrels (Maser et al., 1986) and birds (Pettersson et al., 1995), and can harbor diverse communities of invertebrates (Stubbs, 1989; Bokhorst et al., 2015). *Bryoria* and other hair lichens also contribute to epiphytic biomass in boreal forests (Campbell & Coxson, 2001) where their eventual decomposition is important to forest nutrient cycling (Pike, 1978; Coxson & Curteanu, 2002). Therefore understanding the health of *Bryoria* is central for understanding the health of the organisms with which they are linked.

Assessing the health of hair lichens can be a difficult task owing to the fact that lichens arise as a result of interactions between many disparate lineages of essentially microbial life forms (Ahmadjian, 1993; Spribille et al., 2020). Potentially pathogenic fungi have been isolated from healthy lichens (Petrini et al., 1990), but whether this could be the case for *Bryoria* remains to be thoroughly investigated. The presence of lichen-associated, or "lichenicolous", fungi (Hawksworth, 1983; Jeffries & Young, 1994; Lawrey & Diederich, 2003) has been used to

measure the health of a given lichen (Hawksworth, 1977; Gilbert, 1988). This is because lichenicolous fungi can produce discolorations, lesions, or dead areas on their lichen hosts (Lawrey & Diederich, 2003). However, beyond floristic or taxonomic studies, this group of fungi has not received much attention historically, and consequently much of their biology is still unknown. Interactions between the most pathogenic, or necrotrophic, lichenicolous fungi and their lichen hosts remain the best understood because they produce visible necroses on their hosts and kill them outright (Jülich, 1972; Hawksworth, 1977; Jülich & Stalpers, 1980; Jeffries & Young, 1994; Yurchenko & Golubkov, 2003). Other lichenicolous fungi exist in a commensal or "parasymbiotic" state (Lawrey & Diederich, 2003) where they can be visibly present on the host body, or "thallus", but are not associated with prominent discolourations or lesions (Rambold & Triebel, 1992).

Typical, healthy *Bryoria* thalli are free-flowing and knotless (Plate 1). However, in many Bryoria populations, it is common to find thalli clumping together and forming brittle dead zones, or "rattails", especially near the terminal ends of thalli (Plate 2). Mass dieback of *Bryoria* has been previously reported and found to be associated with unusually heavy and prolonged rain events in conifer forests in Norway and British Columbia (Goward 1998; Gauslaa 2002, 2014). These previous reports on *Bryoria* provide important connections between the ecophysiology of hair lichens with their health and were fundamental to the progress of this project. During the course of this study I found *Bryoria* rattails in all seasons, and in winter months these rattails were associated with an apparently cold-tolerant mold discovered by Toby Spribille in January 2019 in British Columbia (Plates 3 & 4). This contrasts with the Norwegian die-back event, in which no pathogenic mycelia were detected on *Bryoria* thalli (Gauslaa, 2002). Whether *Bryoria*

die-back events are commonplace and whether such events are driven by pathogens, physiological processes, or some combination of both is unknown.

In my thesis, I focus on investigating the role pathogens play in *Bryoria* dieback in western Canada. Specifically, the objectives for this study are to 1) identify the lichen pathogen or pathogens associated with the formation of *Bryoria* rattails, 2) determine whether the infection shows any patterns of lichen-host preference, and 3) assess whether the pathogen could exist as a cryptic, asymptomatic fungal symbiont, such has been recently reported for other lichens (Spribille et al., 2016; Tuovinen et al. 2019).

2 MATERIALS AND METHODS

2.1 Field collection

To collect material representing healthy and unhealthy hair lichens, and other potentially infected macrolichens, I surveyed boreal and montane conifer forests for *Bryoria* in western Canada and the northwestern United States. Hair lichen visibly infected with mold were collected in British Columbia, Alberta, Saskatchewan (Canada), Montana, and Idaho (USA) between 2019 and 2020 (Table 1, Fig. 1). Surveys were conducted from a range of elevations, from 130 meters to 1935 meters above sea level (Table 1, Fig. 1). Conifer trees in the genera *Picea, Abies,* and *Pseudotsuga* were the typical phorophytes of *Bryoria* collections. To determine whether the pathogen was present in Europe, additional collections were made by Toby Spribille in Sweden and Austria during the summer of 2019 (Table 1, Fig. 1). Only epiphytic lichens that were within standing reach (approximately 1 - 2.7 m) were collected. The upper canopy was never accessed for sampling. Infected lichens were categorized in two ways: as either material which had fallen to the ground (Plate 5) or material which was still epiphytic.

Owing to the ecological differences between soil surface and above-ground environments, I hypothesize that different fungal species would infect epiphytic versus fallen lichen material. Material that had fallen to the ground was collected opportunistically. Collection sites were selected by utilizing BING Maps (www.bing.com/maps). A map of all collections from this study (Fig. 1) was made using QGIS v2.18 (QGIS.org) with a WAD-84 coordinate reference system and the North Pole Lambert Azimuthal Equal Distance projection.

2.2 DNA extraction and sequencing - Pathogen

To identify the pathogen causing rattails in *Bryoria*, I extracted, amplified, and sequenced its DNA. Hyphae or, when present, basidiome tissue from the mold was separated from lichen-host material using an Olympus SZX16 dissecting scope prior to DNA extraction. Extractions were performed using the DNeasy Plant Mini Kit (QIAGEN, Hilden, Germany) per the manufacturer's instructions. Special attention was paid to reduce the amount of host tissue included in each extraction as excess lichen material gummed up the spin columns.

As host tissue could not be completely separated from the mold, I designed pathogen-specific markers for two loci – the internal transcribed spacer region (ITS) and the translation elongation factor 1-α (EF1-α) (Table 2). I chose these two loci because ITS is a commonly sequenced gene region for fungi (Schoch et al., 2012) and EF1-α is a variable gene region that has been shown to be informative when constructing molecular phylogenies (Roger et al., 1999). In addition, comparable sequence data for EF1-α were available via GenBank. These primers were designed by initially performing PCR with more general fungal ITS (White et al., 1990; Gardes & Bruns, 1993) and EF1-α primers (Rehner & Buckley, 2005), then extracting all positive bands from the electrophoresis gel with the QIAquick Gel Extraction Kit (QIAGEN,

Hilden, Germany) to be sequenced. To ensure that the primers did not amplify other fungal DNA known to be present in hair lichens, I aligned the resulting sequence fragments of the pathogen against publicly available sequences of the host mycobiont, as well as *Cyphobasidium* and *Tremella*, two basidiomycete yeasts known to be asymptomatically present in lichen thalli (Spribille et al., 2016; Tuovinen et al., 2019) using AliView (Larsson, 2014). I used the ThermoFisher Oligo Design Tools web portal (ThermoFisher Scientific, Walten, Massachusetts, USA) to look for nucleotide motifs that discriminate against these other fungal sequences, and to ensure that the primers were chemically usable; specifically, that the primers contained roughly 40-60% GC, melting temperature was not too high, and primers were not self-binding. As a positive control, I re-ran PCRs with these primers using the DNA extractions from which they were initially sequenced. If a single band was produced I submitted the PCR product for sequencing (see below), and used the primers on new DNA extractions of the lichen pathogen.

Five µL dilutions of DNA extract were used in a twenty-two µL reaction with KAPA3G Plant PCR Kit (Millipore Sigma, Burlington, Massachusetts, USA) using the manufacturer's specifications and were run on a Veriti 96-Well Fast Thermal Cycler (Applied Biosystems, Foster City, California, USA) with the following programs for ITS: an initial denaturation at 95°C for 5 minutes, followed by 35 cycles of 95°C for 30 s, 57°C for 30 s, 72°C for 30 s, and a final extension of 72°C for 7 min; and for EF1-α: an initial denaturation at 95°C for 5 min, then nine touchdown cycles of 95°C for 1 min, 66-57°C for 30 s, 72°C for 1 min, then 36 cycles of 95°C for 30 s, 56°C for 30 s, 72°C for 1 min, and a final extension of 72°C for 10 min. Two µL aliquots of PCR product were viewed on 0.8% agarose gels stained with GelRed™ (Biotium, VWR, Hayward, California, USA). All positive bands were enzymatically purified using Exonuclease I and Shrimp Alkaline Phosphatase (New England BioLabs, Inc., Ipswich,

Massachusetts, USA). Sanger sequencing of all PCR products was outsourced to Psomagen (Rockville, Maryland, USA). Initial querying of the sequences against the NCBI nucleotide database using BLAST (Altschul et al., 1990) returned high-scoring hits from the basidiomycete genus *Athelia* Pers. (Atheliaceae). Viacheslav Spirin (University of Helsinki) provided *Athelia* material from collections he made across Eurasia and western North America (Table 1) for me to compare my sequences and specimens against. For this material, only basidiomata tissue was used for DNA extraction using the QIAamp DNA Investigator Kit (QIAGEN, Hilden, Germany). Successful sequence fragments from Psomagen were retrieved electronically, checked for electropherogram ambiguities with BioEdit (Hall, 1999), and subjected to a BLAST (Altschul et al., 1990) search to determine whether their approximate taxonomic grouping was different from the host-lichen identity.

2.3 Morphological analyses of pathogen

In addition to DNA analysis, morphological features were also used to identify the mold. Twenty-two specimens of *Athelia* producing basidiomata (Table 1), sexual structures of basidiomycetes, were included in this study. Fifteen measurements of basidium length, basidium width, sterigma length, sterigma width, basidiospore length, basidiospore width, and hyphal diameter were taken from each specimen. Basidioma squashes were viewed at 1000x on a Zeiss AXIO A.1 microscope and stained with 1% Phloxine-B in 5% potassium hydroxide (KOH), and rehydrated with water as necessary. Microscopic images were taken using an Olympus SC180 Color Camera and all measurements were made using Olympus cellSens software. A one-way analysis of variance (ANOVA) and subsequent Tukey's Honestly Significant Difference post-hoc test (Tukey HSD) were performed on these measurements in R v3.6.1 in RStudio v1.1.463 (R

Core Team, 2019) against mold species identity or species group as determined *a posteriori* to the generation of a phylogenetic tree (see *Phylogenetic analyses*). Multivariate analyses using all specimen measurements were performed with non-metric multidimensional scaling (NMDS) in the R package *vegan* v2.5-6 (Oksanen et al., 2019).

2.4 Host preference and identity

Often numerous species of lichen grow within close proximity to one another so I tested the preference of the rattail pathogen for particular lichen hosts. For this study, each macrolichen found to be visiblly infected was identified to species or genus level using morphological and chemical characters (Brodo & Hawksworth, 1977; Goward et al., 1994; Goward, 1999; Myllys et al. 2011). In order to determine the identity of diagnostic secondary metabolites present within the host lichens, I performed chemical spot tests with potassium hydroxide, sodium hypochlorite, and *para*-phenylenediamine along with thin layer chromatography (TLC) in solvent solutions A and B according to Orange et al. (2001). The identification to species level of one group of lichen hosts, *Bryoria* sect. *Implexae* (Gyeln.) Brodo & D. Hawksw., is quite difficult using morphological characteristics or chemical techniques. Accordingly, DNA extractions of uninfected tissue for lichens within this group were amplified using markers for ITS, the intergenomic spacer (IGS), and glyceraldehyde-3-phosphate dehydrogenase (GAPDH), following a previous study on this group by Velmala et al. (2014) (Tables 3 & 4). Extractions were performed using the DNeasy Plant Mini Kit (QIAGEN) as per the manufacturer's instructions. Subsequently, five µL dilutions of DNA extract were used in a twenty-two µL PCR reaction with KAPA polymerase (Millipore Sigma) and run on a Veriti 96-Well Fast Thermal Cycler (Applied Biosystems) using the following programs for ITS: an initial denaturation at

95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 57°C for 30 s, 72°C for 30 s, and a final extension of 72°C for 7 min; IGS: initial denaturation at 95°C, followed by 35 cycles of 95°C for 30 s, 55°C for 30 s, 72°C for 1 min, and a final extension of 72°C for 7 min; GAPDH: an initial denaturation at 95°C for 5 min, then 5 cycles of 95°C for 30 s, 56°C for 30 s, 72°C for 1 min, then 30 cycles of 95°C for 30 s, 54°C for 30 s, 72°C for 1 min, and a final extension of 72°C for 10 min (Velmala et al., 2014). From each reaction, two µL aliquots of PCR product were viewed on 0.8% agarose gels stained with GelRed™ (Biotium, VWR). All positive bands were enzymatically purified using Exonuclease I and Shrimp Alkaline Phosphatase (New England BioLabs, Inc.). Sanger sequencing of all PCR products was outsourced to Psomagen (Rockville, Maryland, USA). The electropherograms of successfully sequenced fragments were viewed on BioEdit (Hall, 1999) and subjected to initial BLAST (Altschul et al., 1990) analysis as mentioned above.

2.5 Latent symbiosis assessment

To test whether the fungal pathogen was present in apparently uninfected asymptomatic *Bryoria,* the pathogen-specific primers (Table 3) were used on 55 DNA extractions from healthy lichen material. I collected these healthy lichens in 2018, prior to the detection of the lichen mold. DNA extractions of six rattailed and visibly infected *Bryoria* specimens were included as positive controls.

2.6 Phylogenetic analyses

To delimit species identity of the mold and *Bryoria* sect. *Implexae* hosts, I constructed phylogenetic trees using a maximum likelihood (ML) approach. Sequences from the mold and *Bryoria* sect. *Implexae* were handled separately, but followed the same general protocol.

Each set of sequences were aligned with MAFFT v7 (Katoh & Standley, 2013), concatenated, and trimmed using custom python scripts developed by Resl (2015) and were implemented following Resl et al. (2015). The resulting alignments were manually edited using AliView (Larsson, 2014). Nucleotide substitution models were determined for each locus using PartitionFinder v2.1.1 (Lanfear et al., 2016). For the protein-coding genes (EF1-α and GAPDH), substitution models were determined individually for the first, second, and third codon positions (Tables 5 & 6). Maximum likelihood analysis was performed in IQ-TREE v2.0 (Nguyen et al., 2015). Branch supports were obtained with ultrafast bootstrapping (Hoang et al., 2018) of 1000 replicates. Only the branches which received ultrafast bootstrap values ≥ 95% were considered well supported (Nguyen et al., 2015). Calculations for the number of variable and parsimonious sites as well as nucleotide composition were generated by IQ-TREE v2.0 (Nguyen et al., 2015). The resulting consensus tree topology was subjected to an Approximately Unbiased (AU) Test (Shimodaira, 2002) in IQ-TREE v2.0 with 1000 bootstrap replicates to evaluate possible alternative topologies based around substrate use (Figs. 2-4). Phylogenetic trees were visualized using FigTree v1.4.3 (Rambaut, 2014).

I also generated haplotype networks for the fungal pathogen to investigate patterns of genetic variation among the pathogen sequences in order to help with species delimitation. After I discarded sequences with ambiguous bases from each alignment, I generated haplotype networks from ITS and EF1-α using the R package *pegas* v0.12 (Paradis, 2010). Subsequently, the average pairwise nucleotide differences among sequence samples (Nei & Kumar, 2000)

within and between haplotype groups was calculated via the "nucleotideDivergence" function in the R package *strataG* v2.4.905 (Archer et al., 2016).

3 RESULTS

3.1 Pathogen identity and substrate preference

Based on morphology and phylogenetic analysis, the pathogen associated with the formation of rattails appeared to belong to the genus *Athelia*. A total of 98 new sequences of *Athelia* were produced for this study, including 66 ITS sequences and 32 EF1-α sequences (Table 1). The final concatenated alignment consisted of 1738 characters (ITS: 685; EF1-α: 1053), with 734 variable and 369 parsimony informative sites (Fig. 5). Based on AICc score and returned log likelihood values, each individual codon position for ITS and EF1-α ran with separate evolutionary models (Table 5). The topologies of each gene tree (Figs. 6 & 7) and the concatenated tree (Fig. 5) support a lineage of lichen-associated pathogens in *Athelia,* which includes all epiphytic material collected in North America for this study – except isolates SG357 and SG414 (see below) – as well as one European isolate from Sweden (SG624). This lineage was recovered as distinct from another known lichen pathogen, *Athelia arachnoidea* (Berk.) Jülich (Jülich, 1972; Jülich & Stalpers, 1980). One Albertan specimen from fallen, infected lichen material (SG639) was recovered as sister to *A. arachnoidea* in both the concatenated and ITS trees (Figs. 5 & 6). Several isolates from fallen lichen material (SG520, SG519, SG555, SG570, and SG573) and two from epiphytic lichens (SG357 and SG414) group with *A. acrospora* Jülich though this lineage was not phylogenetically well supported (Fig. 5).

Additionally, several species of *Athelia*, as identified on collection packets or previous accessions, were not recovered as monophyletic in any gene tree: *A. epiphylla* Pers., *A. decipiens*

(Höhn. & Litsch.) J. Erikss., *A. bombacina* Pers., and *A. cystidiolophora* Parm. (Figs. 5-7). Individuals identified as *A. cystidiolophora* fail to form a well supported clade but appear with named sequences of *A. decipiens* and *A. epiphylla* (Figs. 5 & 6). Morphologically, *A. cystidiolophora* is quite distinct from other *Athelia* since it is one of two species which produce cystidia – diagnostic hyphal projections present in many basidiomycetes (Jülich, 1972; Jülich & Stalpers, 1980). Sequences from previously identified specimens of these four species were organized into two poorly supported species groups: Group I consisted of sequences from *A. decipiens, A. epiphylla,* and *A. cystidiolophora*; and, Group II with *A. bombacina* and *A. epiphylla* (Fig. 5). The position of one sample from fallen lichen material (SG518) was found as sister to Group I – *A. epiphylla* material in the EF1-α tree with 100% ultrafast bootstrap support (Fig. 7), unsupported but within Group I in the concatenated tree (Fig. 5), and was unsupported and unplaced in the ITS tree (Fig. 6).

Substrate preference did not entirely explain species relationships within *Athelia*. This contradicts my prediction that the fungal pathogens from lichen material on the ground would be a different species than on lichens which were still epiphytic. However, one of the powers of phylogenetics lies in our ability to test our hypotheses – represented here as gene trees produced during this study. I tested the probability of alternative tree topologies using the Approximately Unbiased (AU) test (Shimodaira, 2002). I created alternative trees to reflect *a priori* patterns I had observed among my samples. Specifically that monophyly would be a reflection of substrate use at time of collection for each *Athelia* (Figs. 2-4). For instance, that all epiphytic lichen-associated specimens would form a single clade, with the same being true for all fallen lichen-associated specimens and all wood associated specimens. I then used the AU test to determine if the constrained alternative trees could be rejected (p-AU < 0.05) or not (p-AU > 0.05). Any tree

with a p-AU < 0.05 would lead me to believe that that tree shape probably cannot be produced with my data, and is a rejectable alternative. For the AU test the null hypothesis would be that all trees are equally probable explanations of my data.

None of the substrate constraints (Figs. 2-4) were found to be probable alternatives to the original topology on the basis that each p-AU ≤ 0.05 (Table 7). This suggests that substrate use at time of collection is, by itself, not an adequate predictor of relationships between these species of *Athelia*.

As an additional measure to delimit species based on genetic variation, I calculated the nucleotide divergence between and within *Athelia* species' haplotypes. Average pairwise differences between the lichen-associated *Athelia* lineage and all other species groups was greater in EF1-α than ITS with values of 0.08715 and 0.07159 between Group II and Group I respectively (Tables 8 & 9), whereas ITS average pairwise distance values ranged from 0.01863–0.04392. The mean nucleotide differences within the lichen-associated *Athelia* lineage were comparatively similar for ITS and EF1-α at 0.02000 and 0.019128, respectively, and represent the lowest mean difference values within any group except for the ITS of Group II (0.0182). The slightly higher within-group differences for the lichen-associated *Athelia* lineage may be a reflection of the highly supported split of isolates SG441 and SG550 as being sister to the lichen-associated *Athelia* lineage (Fig. 5).

All of the lichen-associated *Athelia* producing mature basidiomata were collected in cold, wet months of mid-late winter, often in the presence of snow (Larsen et al., 1981; Plate 5; Table 1). At other times of the year, only asexual sclerotia or hyphae were detectable on rat-tailed *Bryoria* (Plate 6). Following the ANOVA (Table 10) and Tukey HSD post hoc test, specimens of the lichen-associated *Athelia* have significantly longer (mean: 51.68 µm, ±0.24 µm, max: 26.07

µm, min: 9.69 µm) and wider basidia (mean: 15.4 µm, ±0.05 µm, max: 7.36 µm, min: 4.03 µm), longer sterigmata (mean: 4.37 µm, ±0.13 µm, max: 12.39 µm, min: 1.06 µm), and wider basidiospores (mean: 3.26 µm, ±0.05 µm, max: 6.09 µm, min: 2.2 µm) than the other specimens measured (Figs. 8 & 9). Considerable overlap of the morphological measurements between species groups can be seen in the NMDS with no distinct patterns emerging (Fig. 10). The lichen-associated *Athelia* lineage overlapped considerably in ordination space but not entirely with the other species groups. Distinguishing *A. acrospora* measurements from those in Group I, Group II, or the lichen-associated *Athelia* using the NMDS was not possible. It is important to note that certain morphological characteristics (e.g., basidiospore shape or presence/ absence of cystidia) could not be included in this form of analysis. Specimen VS 9717 was excluded from the NMDS because a complete number of measurements for hyphal diameter could not be obtained due to lack of usable material.

3.2 Patterns of host preference

Only lichens in the family Parmeliaceae collected for this study were found to be infected by *Athelia* (Table 11). Within Parmeliaceae, lichens in the genus *Bryoria* were most frequently encountered as hosts representing 62.5% of all collected infected lichens (Table 11). Among *Bryoria,* the majority of detected infections were found on individuals in section *Implexae*. A total of 94 new sequences of *Bryoria* sect. *Implexae* were produced for this study, including 20 ITS sequences, 36 IGS, and 38 GAPDH sequences (Table 12). The final concatenated alignment consisted of 2018 characters (ITS: 513; IGS: 391; GAPDH: 1024), with 469 variable and 118 parsimony-informative sites (Fig. 11). The optimal *a priori* partitioning scheme (based on AICc score and returned log likelihood value) was to segregate ITS, IGS, and individual codon

positions of GAPDH of *Bryoria* sect. *Implexae* with separate evolutionary models (Table 6). Within *Bryoria* sect. *Implexae,* no species groups were preferred hosts over any other (Fig. 11; Table 13).

3.3 The mold as a cryptic symbiont

Of the 55 specimens screened, no healthy *Bryoria* tested positive for the cryptic presence of *Athelia*, whereas all six rattail positive controls produced *Athelia* sequences (Table 1; Fig. 5)

4 DISCUSSION

4.1 Rattails and Athelia

The results indicate that the formation of rat-tailed *Bryoria* is strongly associated with the infection and subsequent winter growth of a novel species of *Athelia,* provisionally presented here as *Athelia seborrheica* sp. nov. pending formal publication (see *Taxonomy* p. 21; Plate 6). This mold has been found to infect only lichens in the family Parmeliaceae. Members of *Bryoria* sect. *Implexae* were found to be most frequently infected (Table 11). *Athelia seborrheica* is found on lichens still epiphytic as well as those which have fallen to the ground. Some but not all infected ground material could be placed within *A. seborrheica* (Fig. 5). Several isolates (SG520, SG519, SG555, SG570, SG573) could be assigned to *Athelia acrospora* based on sequence data, though no developed basidiomata were observable to determine their morphological affinity (Fig. 5). The placement of one isolate in particular, SG518, was poorly resolved across the concatenated and ITS gene trees (Figs. 5 & 6). However, in the EF1-α tree SG518 was found as sister to Group I/ *A. epiphylla* with significant bootstrap support (Fig. 7). The behavior of SG518 sequences across the three trees may be a reflection of incomplete lineage sorting or

incongruence between the gene trees generated (Dávalos et al., 2012), or could reflect poor quality of the ITS sequence for this isolate. If the former issue is true, then sampling additional loci, adding more taxa, or evaluating different character states for *Athelia* could resolve the unsupported relationships in these trees (Dávalos et al., 2012).

It is important to note that epiphytic *Bryoria* thalli can be classified in two ways: those which are anchored to the bark of the tree, and those which have fallen from above and have become draped over lower branches (Goward, 1998). Draped *Bryoria* falling from the upper canopy onto lowers branches of the tree occupy a suboptimum habitat (Goward, 1998; Goward, 2003). Therefore, draped *Bryoria* might be more preferentially infected than those anchored, but because I did not classify my collections as draped or attached at the time they were collected I cannot address this with certainty. Whether lichens higher in the canopy are infected by *Athelia* or other fungi is unknown. Additionally, lichen decomposition could be a successional process. While *A. seborrheica* may initially degrade epiphytic lichen thalli, other microbes may be responsible for the later stages of its eventual breakdown once it reaches the ground (Coxson & Curteanu, 2002). *A. seborrheica* collected from fallen lichen thalli could have been present earlier in this successional process.

From sequence data, *A. seborrheica* seemed most closely related to *A. acrospora*, a wood decaying fungus not previously known to infect lichens, and *A. epiphylla*, the type species of the genus. Once reproductive individuals were found, the basidiospores and basidia of *A. seborrheica* were easily differentiated from *A. acrospora* in that the basidiospores of *A. acrospora* are much longer than wide (Jülich, 1972; Jülich & Stalpers, 1980) and its basidia are often smaller than what was observed in specimens of *A. seborrheica* (Table 14; Plate 6). The basidia of *A. epiphylla* are slightly shorter and wider than *A. seborrheica*, and *A. epiphylla* has

basidiospores which are larger and narrower than *A. seborrheica. Athelia arachnoidea*, another commonly reported lichen pathogen, is also easily distinguished morphologically from *A. seborrheica*. *Athelia arachnoidea* is often two-sterigmate, and has much larger basidiospores and basidia than *A. seborrheica* (Table 14; Jülich, 1972; Jülich & Stalpers, 1980).

The monophyly of *A. acrospora* or *A. epiphylla* was not supported in any tree produced in this study. Indeed, *A. epiphylla* represents a species complex in need of revision, the broad range of morphological forms of which could be mistaken for other species including but not limited to *A. acrospora* and *A. arachnoidea* (Jülich, 1972; Eriksson & Ryvarden, 1973; Jülich & Stalpers, 1980; Ginns & Worrall, 1999; Hawksworth, 2003). The polyphyletic nature of the other *Athelia* species may be a reflection of errors introduced by misidentification of herbarium material and GenBank deposits (Hofstetter et al., 2019). I was unable to examine type material of *A. epiphylla* (National Herbarium of the Netherlands in Leiden) or *A. acrospora* (Swedish Museum of Natural History in Stockholm), or GenBank vouchers UC2022957, UC 2022961, UC 2022960, UC 2022956, and UC 2022976 (University of California, Berkeley) because these specimens were unavailable for loan. *Athelia epiphylla* merits a proper phylogenetic re-examination (V. Spirin, University of Helsinki, pers. comm.) but that is beyond the scope of this study.

Knowing the species relationships and evolutionary history of *Athelia* is fundamental to follow-up investigations regarding this cosmopolitan genus of pathogens. Several species of *Athelia* are known as facultative pathogens of lichens (Diederich et al., 2018), but *Athelia* also contains economically important agricultural pests (Adams & Kropp, 1996). However, little phylogenetic information on this genus is available save studies on crop pests (Harlton et al., 1995; Adams & Kropp, 1996; Okabe & Matsumoto, 2003; Xu et al., 2010), a study of all

homobasidiomycetes associated with lichens in which *A. arachnoidea* was the only *Athelia* species included (Lawrey et al., 2007), and a report of an *Athelia* whose sclerotia – or asexual hyphal masses – mimic termite eggs (Matsuura et al., 2000). The phylogenetic trees produced in this study represent the largest sample of *Athelia* and will help bridge significant knowledge gaps for this genus.

It has been reported that *A. arachnoidea* depletes lichen thalli of nutrients via haustorial contact with the algal symbionts (Yurchenko & Golubkov, 2003). I was unable to determine how *Athelia seborrheica* was obtaining nutrients as no haustoria were visible from any of the microscopy that was performed during the course of this study. Lawrey and Diederich (2003) hypothesize that generalist parasites, such as *Athelia,* could possess a wide range of enzymes for the digestion of commonly found host material. Two groups of enzymes have been characterized in *Athelia* (*Sclerotia*) *rolfsii* and appear to play a key role in its infection of plant cellular material: cellobiose dehydrogenases (Baminger et al., 2001) and mannanases (Großwindhager et al., 1999). Cellobiose dehydrogenases are found in many wood-degrading species of fungi and are principally involved in the degradation of cellulose and/ or lignin (Baminger et al., 2001). The expression of mannan-degrading enzymes in *Athelia rolfsii* can be induced when glucose is the form of carbon available to fungal cultures of the pathogen (Großwindhager et al., 1999). However, other classes of mannanases can be expressed only when *A. rolfsii* is grown in cellulose media, indicating that the mold possesses a complex suite of enzymes to continuously degrade host material as different carbon sources are gradually used up (Großwindhager et al., 1999). It is unknown how *A. seborrheica* gains nutrients from its host. It could be parasitizing the photosynthesizing partner and/or fungal partners, or it might be tapping into the mannans, or other polysaccharides, which comprise the extracellular matrix of the lichen cortex (Spribille et

al., 2020). Alternatively it could be performing a combination of the three: moving from one nutritional aspect of its host to the next as it slowly exhausts each portion of the lichen (Plate 4).

4.2 Bryoria *section* Implexae

The majority of lichens found to be infected by *Athelia seborrheica* belonged to *Bryoria* sect. *Implexae* (Table 11). Differentiating individual species in this section relies on a balance of chemical, ecological, morphological, and molecular techniques (Velmala et al., 2014; Boluda et al. 2015, 2019). However, as is the case with most lichenological studies, molecular techniques are often employed for only the main mycobiont, or fungal partner, as a proxy for the lichen as a whole (Spribille, 2018). A previous study on *Bryoria* sect. *Implexae* found relationships within this group could be explained by broad geographical patterns as well as chemistry and morphology (Velmala et al., 2014), specifically that the lecanoromycete can be split into clades which are either European, North American, or more globally distributed (Velmala et al., 2014). Species concepts and data (i.e., sequences, chemistry, and morphology) from that study (Velmala et al., 2014) were the basis for the phylogenetic approach I used to determine which species of *Bryoria* sect. *Implexae* I had collected (Tables 4 & 13). However, the concatenated tree that I generated failed to support the same geographical distributions as being explanatory for species identity within sect. *Implexae* (Fig. 11). Additionally, no patterns of chemistry or morphology were reflected in the concatenated tree (Table 13; Fig. 11). The loci that I used (ITS, IGS, and GAPDH) appear to be under-informative. It could be argued that providing additional loci for the main mycobiont may be a useful way to disentangle this group more fully. However, when a recent study expanded the molecular dataset with two additional loci (FRBi15 and FRBi16) and

18 microsatellite markers, the authors still found a major mismatch between genetic relationships and the phenotypes of these *Bryoria* (Boluda et al., 2019).

Many of the species formerly accepted in *Bryoria* sect. *Implexae* have been synonymized with *B. fuscescens* (Boluda et al., 2019), though the chemical and morphological variation in *B. fuscescens* remains unexplained. It is apparent that the diverse chemistry, ecology, and morphology within *Bryoria* sect. *Implexae* have not been elucidated by previous phylogenies of the mycobiont (Boluda et al., 2015, 2019), a phenomenon Spribille (2018) referred to as the "phantom phenotype". To examine the lichen only in terms of its mycobiont is to miss the entire symbiosis it embodies (Goward, 2008). Surveying additional symbionts associated with *Bryoria* sect. *Implexae* – yeasts, bacteria, algae – could help to disentangle the evolutionary history of this group of lichens (Spribille, 2018).

4.3 Cryptic symbiosis

Athelia does not appear to be a cryptic, asymptomatic partner in hair lichen symbioses. I tested whether this fungal pathogen could be a dormant, potentially mutualistic or commensal partner that only begins to infect *Bryoria* as a result of some intrinsic symbiotic imbalance. This does not appear to be the case for *Athelia* since no healthy looking hair lichen tested positive for the presence of this fungus. I was driven to this line of investigation by recent studies that have found basidiomycete yeasts embedded within the cortices of ascomycete lichens, raising important questions regarding the nature of lichen symbiosis (Spribille et al., 2016, Tuovinen et al., 2019). I only tested for the presence of *Athelia*; whether other fungal pathogens could be intrinsic to these symbioses remains to be investigated.

5 CONCLUSION

Here I provide the first report of the pathogenic infection of *Bryoria* by a new species of mold, *Athelia seborrheica*. Whether or not this widespread infection of *Bryoria* in western North America is a recent event or simply an overlooked phenomenon is difficult to determine with certainty since using historical collections to assess the health of *Bryoria* over time was unfeasible for this study. Understanding the health of *Bryoria* and other hair lichens is essential to understanding the health of the forests they inhabit and the animals with which they interact, notably the herds of woodland caribou which depend upon them as a crucial winter food source (Edwards et al., 1960; Rominger et al., 1996; Thomas et al., 1996; Johnson et al., 2000). This research serves as the historic benchmark for documenting a pathogenic outbreak affecting an ecologically significant lichen genus.

6 TAXONOMY

Athelia seborrheica Goyette & T. Sprib. **sp. nov.**
Type: USA, Montana, Edna Creek Rd. area (48°40.391'N, 115°01.109'W), on *Bryoria* section *Implexae* epiphytic on *Abies lasiocarpa,* 7 April 2019, S. Goyette 633 (DNA isolate SG524; holotype: University of Alberta Herbarium [ALTA]; isotypes: Canadian Museum of Nature [CANL], University of Helsinki [H])

<u>Diagnosis</u>
Differing from *Athelia arachnoidea* in its shorter basidia usually with four sterigmata, from *A. acrospora* in its stouter basidiospores, and from *A. epiphylla* in its slightly longer though narrower basidia, wider basidiospores, and preferential infection of hair lichens in Parmeliaceae.

<u>Description</u>

Basidiomata effuse. Hymenial surface cottony, eggshell to creamy white. Context white, thin (<100 µm), texture indistinct. Margin white, densely cottony to arachnoid, hyphal strands present. Hymenial surface whitish, indistinct. Hyphae monomitic with clamps at septa. Hyphae hyaline, cylindrical, 2–3 µm in diameter, rarely encrusted with crystals. Cystidia absent. Basidia hyaline, cylindrical to clavate when mature, 14–18.5–(20) x 5.5–6–(7) µm, smooth surfaced, with four – seldom two – equally elongate sterigmata 3.5–5.5 x 1–1.5 µm. Basidiospores thin-walled, hyaline, ovate with rounded base and prominent apiculus, 4.5–5.5 x 3–3.5–(4.5) µm, occasionally sticking together.

Habitat

Preferred substrates are hair lichens in the Parmeliaceae, specifically *Bryoria* sect. *Implexae*. Seldom found on bark of *Abies lasiocarpa* in lichen-rich forests. Abundant in western North America with one specimen lacking a basidioma (isolate SG624) from eastern Sweden.

Etymology

From seborrhea, a discharge of oily matter which can manifest as a severe form of dandruff characterized by inflammation and flaking of skin from the scalp, nose, and eyebrows.

Commentary

GenBank accession KP814332 represents an ITS sequence from specimen UC 2022957 (Rosenthal et al., 2017) derived from "litter or well decayed wood in pinaceous forest" and was collected in Oregon, USA. This specimen was requested on loan but was unavailable for study. The sequence differs in 1 position and is likely referable to *A. seborrheica*.

Additional Specimens Examined (*Athelia seborrheica*):

CANADA. ALBERTA: Athabasca County, 4 Jun 2018, S Goyette 522 (DNA isolate SG426); ~1-1.5 km from HWY to Fort McMurray backroad, 20 Apr 2018, S Goyette 299 (DNA isolate SG410); Lily Lake Trail, 25 May 2019, T Spribille (DNA isolate SG567); Marten Lakes Wilderness Campus, 22 Sep 2018, S Goyette 581 (DNA isolate SG441); Marten Lakes

Wilderness Campus, 23 Sep 2018, S Goyette 583 (DNA isolate SG436); Marten Lakes Wilderness Campus, 21 Sep 2019, S Goyette 648 (DNA isolate SG641); before Marlboro, 23 Feb 2018, S Goyette 625 (DNA isolate SG493); Mukiki Lake, 18 May 2019, S Goyette 638 (DNA isolate SG542); Mukiki Lake, 18 May 2019, S Goyette 643 (DNA isolate SG564); outside of Mukiki Lake, 18 May 2019, S Goyette 641 (DNA isolate SG562); north of Rock Island Lake, 26 Apr 2019, T Spribille (DNA isolate SG560); off HWY 43 before Whitecourt, 10 Jul 2018, S Goyette 536 (DNA isolate SG450); Yellowhead County, 18 May 2019, S Goyette 639 (DNA isolate SG548); Yellowhead County, 18 May 2019, S Goyette 640 (DNA isolate SG550). BRITISH COLUMBIA: outside Chinook Cove, T Spribille (DNA isolate SG455); outside Chinook Cove, T Spribille (DNA isolate SG459); outside Chinook Cove, T Spribille (DNA isolate SG461); Crystal Ridge area, Valemount, 17 Mar 2019, S Goyette 627 (DNA isolate SG505); Coquihalla Pass, 11 May 2019, T Spribille (DNA isolate SG556); Coquihalla Pass, 11 May 2019, T Spribille (DNA isolate SG558); Coquihalla Pass, 11 May 2019, T Spribille (DNA isolate SG572); past Falkland, T Spribille (DNA isolate SG456); past Falkland, T Spribille (DNA isolate SG458); past Falkland, T Spribille (DNA isolate SG460); Little Lost Lake trail loop, 11 May 2019, S Goyette 646 (DNA isolate SG635); Upper Clearwater Valley, 28 Aug 2019, T. Goward 19-154 (DNA isolate SG653); Upper Clearwater Valley, 28 Aug 2019, T. Goward 19-155 (DNA isolate SG656). SWEDEN: UPPLAND, Vänge parish, T Spribille (DNA isolate SG624). USA. IDAHO: outside of Lolo Pass, S Goyette 626 (DNA isolate SG498). MONTANA: Edna Creek Rd. area, 7 Apr 2019, S Goyette 631 (DNA isolate SG512); Edna Creek Rd. area, 7 Apr 2019, S Goyette 636 (DNA isolate SG527); Edna Creek Rd. area, 7 Apr 2019, S Goyette 637 (DNA isolate SG528); outside Edna Creek Rd. area, 7 Apr 2019, S Goyette 632 (DNA isolate SG521); outside Edna Creek Rd. area, 6 Apr 2019, S Goyette 634 (DNA isolate SG525); outside Stryker, 6 Apr 2019, S Goyette 629 (DNA isolate SG507); outside Stryker, 6 Apr 2019, S Goyette 635 (DNA isolate SG526); outside Stryker/ Stillwater, 6 Apr 2019, S Goyette 645 (DNA isolate SG574); outside of Stryker, 6 Apr 2019, S Goyette 628 (DNA isolate SG506); outside of Stryker, 6 Apr 2019, S Goyette 630 (DNA isolate SG510). WASHINGTON: Clallam Co., Hurricane Ridge, 19 Sep 2014, VS 8747 (DNA isolate SG588). Note: All specimens are deposited in ALTA except T. Goward 19-154 (DNA isolate SG653) and T. Goward 19-155 (DNA isolate SG656), which are in the Beaty Biodiversity Museum [UBC].

Comparison Material Examined (*Athelia acrospora*):

CANADA. ALBERTA: outside Nojack, 9 May 18, S Goyette 393 (DNA isolate 414). BRITISH COLUMBIA: Coquihalla Pass, C, 11 May 2019, T Spribille (DNA isolate SG555); Coquihalla Pass, 11 May 19, T Spribille (DNA isolate SG573); outside Lower Goat River Trail, 12 May 19, S Goyette 644 (DNA isolate SG570); Trophy Mountain, 9 Jun 18, S Goyette 525 (DNA isolate SG357). SASKATCHEWAN: near La Ronge, 28 Apr 18, T Spribille (DNA isolate SG519); near La Ronge, 28 Apr 18, T Spribille (DNA isolate SG520). USA. WASHINGTON: Pend Oreille Co., Gypsy Meadows, 17 Oct 2014, VS 8701a (DNA isolate SG586).

Comparison Material Examined (*Athelia arachnoidea*):

AUSTRIA. STYRIA: Kainbach bei Voitsberg, T Spribille (DNA isolate SG621).

Comparison Material Examined (*Athelia bombacina*):

CANADA. ALBERTA: outside of Mukiki Lake, 18 May 19, S Goyette 642 (DNA isolate SG563).

Comparison Material Examined (*Athelia cystidiolophora*):

RUSSIA. NIZHNY NOVGOROD REGION: Lukoyanov Dist., Panzelka 26 July 2018, VS 12063 (DNA isolate SG601); Bogorodsk Dist., Krastelikha 5 Sept 2011, VS 4442 (DNA isolate 603). LENINGRAD REGION: Podporozhie Dist., Vazhinka, 16 Sept 2017, VS 11390 (DNA isolate SG600).

Comparison Material Examined (*Athelia decipiens*):

RUSSIA. KHABAROVSK REGION: Verkhnebureinskii Dist., Kyvyty 17 Aug 2014, VS 7395 (DNA isolate SG597). NIZHNY NOVGOROD REGION: Bogorodsk Dist., Krastelikha 2 Oct 2015, VS 9867 (DNA isolate SG604); Lukoyanov Dist., Sanki 20 Aug 2015, VS 9737 (DNA isolate SG610); Lukoyanov Dist., Sanki Reg., 4 Aug 2017, VS 11357 (DNA isolate SG596).

Comparison Material Examined (*Athelia epiphylla*):

CANADA. ALBERTA: East of Devon, Small tributary of North Sask River, 16 June 1999, UA10144 (DNA isolate SG615); Yellowhead County, Whitehorse Wildland Provinical Park, 26 July 2015, VS 8961 (DNA isolate SG582); Yellowhead County, Whitehorse Wildland Provinical Park, 26 July 2015, VS 8958 (DNA isolate SG593). RUSSIA. LENINGRAD REGION: Boksitogorsk Dist., Chagoda, 9 May 2018, VS 11884 (DNA isolate SG595). NIZHNY NOVGOROD REGION: Boksitogorsk Dist., Chagoda 9 May 2018, VS 11884 (DNA isolate SG595); Lukoyanov Dist., Sanki, 20 Aug 2015, VS 9719 (DNA isolate SG594).

Comparison Material Examined (*Athelia* sp.):

CANADA. ALBERTA: in string fen near Lac La Biche, S Goyette 647 (DNA isolate SG639). SASKATCHEWAN: near La Ronge, 28 Apr 18, T Spribille (DNA isolate SG518).

Note: ITS and EF1-α sequences from specimen S Goyette 647 (DNA isolate SG639) were sister to *A. arachnoidea* sequences in all gene trees. The length of the branch between this specimen and the *A. arachnoidea* was long suggesting that it represents a separate species. No mature basidiomata were present to determine the identity of this specimen.

7 TABLES, FIGURES, and PLATES

Table 1 Voucher table for *Athelia* collected and sequenced for this study. Type specimen for *Athelia seborrheica* (S Goyette 633, extraction number SG524) is in bold. Final GenBank accession numbers for the ITS and EF1-α will be obtained upon formal submission of the publication. Successfully sequenced loci are indicated with an "x".

Genus species	Extract ID	Locality	Elevation (m)	Collection number	Substrate	Lichen Host	Latitude	Longitude	Basidioma measured?	ITS	EF1-α	Notes
Athelia seborrheica	SG410	~1-1.5 km from HWY to Fort McMurray (backroad), Alberta, 20 Apr 2018	592	S Goyette 299	lichen/ epiphyte	*Bryoria* sect. *Implexae*	55°23.596' N	112°28.396'W	No	x		a priori collection and extraction
Athelia seborrheica	SG426	Athabasca County, Alberta, 4 Jun 2018	539	S Goyette 522	lichen/ epiphyte	*Bryoria* sect. *Implexae*	54°57.056' N	112°57.280'W	No	x		a priori collection and extraction
Athelia seborrheica	SG436	Marten Lakes Wilderness Campus, Alberta, 23 Sep 2018	800	S Goyette 583	lichen/ ground	*Bryoria* and *Usnea*	55°36'35.0"N	114°33'35.0"W	No	x	x	

Athelia seborrheica	SG450	off HWY 43 before Whitecourt, Alberta, 10 Jul 2018	700	S Goyette 536	lichen/ epiphyte	*Bryoria fuscescens*	54°06'16.5 "N	115°37'39 .0"W	No	x		a priori collection and extraction
Athelia seborrheica	SG455	outside Chinook Cove, British Columbia	760	T Spribille	lichen/ epiphyte	*Bryoria* sect. *Implexae*	51°15'31.2 "N	120°12'44 .7"W	No	x	x	
Athelia seborrheica	SG456	past Falkland, British Columbia	810	T Spribille	lichen/ epiphyte	*Bryoria* sect. *Implexae* and *Usnea*	50°26'08.4 "N	119°30'17 .7"W	No	x	x	
Athelia seborrheica	SG458	past Falkland, British Columbia	810	T Spribille	lichen/ epiphyte	*Bryoria sect. Implexae* and *Usnea*	50°26'08.4 "N	119°30'17 .7"W	No	x	x	
Athelia seborrheica	SG459	outside Chinook Cove, British Columbia	760	T Spribille	lichen/ epiphyte	*Bryoria sect. Implexae*	51°15'31.2 "N	120°12'44 .7"W	No	x	x	

Athelia seborrheica	SG460	past Falkland, British Columbia	760	T Spribille	lichen/ epiphyte	*Bryoria sect. Implexae*	51°15'31.2 "N	120°12'44 .7"W	No	x	x	
Athelia seborrheica	SG461	outside Chinook Cove, British Columbia	810	T Spribille	lichen/ epiphyte	*Bryoria tortuosa* and *Bryoria sect. Implexae*	50°26'08.4 "N	119°30'17 .7"W	No	x	x	
Athelia seborrheica	SG493	before Marlboro, Alberta , 23 Feb 2018	997	S Goyette 625	lichen/ epiphyte	*Bryoria fremontii*	53°34.065' N	116°42.20 4'W	Yes	x	x	
Athelia seborrheica	SG498	outside of Lolo Pass, Idaho	1280	S Goyette 626	lichen/ epiphyte	*Bryoria fremontii* and *Bryoria fuscescens*	46°47'05.7 "N	114°23'02 .1"W	No	x	x	
Athelia seborrheica	SG505	Crystal Ridge area, Valemount, British Columbia, 17 Mar 2019	960	S Goyette 627	lichen/ epiphyte	*Bryoria sect. Implexae*	52°47'25.7 "N	119°17'30 .3"W	No	x		

Athelia seborrheica	SG506	outside of Stryker, Montana, 6 Apr 2019	1006	S Goyette 628	lichen/ epiphyte	*Bryoria fremontii* and *Bryoria fuscescens*	48°40.302' N	114°45.297'W	No	x	x	
Athelia seborrheica	SG507	outside Stryker, Montana, 6 Apr 2019	1211	S Goyette 629	lichen/ epiphyte	*Bryoria sect. Implexae*	48°41.510' N	114°44.173'W	No	x	x	
Athelia seborrheica	SG510	outside of Stryker, Montana, 6 Apr 2019	1211	S Goyette 630	lichen/ epiphyte	*Bryoria sect. Implexae* and *Nodobryoria oregana*	48°41.510' N	114°44.173'W	No	x	x	
Athelia seborrheica	SG512	Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 631	lichen/ epiphyte	*Bryoria fuscescens*	48°40.391' N	115°01.109'W	Yes	x		
Athelia seborrheica	SG521	outside Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 632	lichen/ epiphyte	*Bryoria sect. Implexae* and *Hypogymnia*	48°40.391' N	115°01.109'W	Yes	x	x	

Athelia seborrheica	**SG524**	**on *Abies lasiocarpa*, Edna Creek Rd. area, Montana, 7 Apr 2019**	**1352**	**S Goyette 633**	**lichen/ epiphyte**	***Bryoria* sect. *Implexae***	**48°40.391' N**	**115°01.109'W**	**Yes**	**x**	**x**	
Athelia seborrheica	SG525	outside Edna Creek Rd. area, Montana, 6 Apr 2019	1211	S Goyette 634	lichen/ epiphyte	*Bryoria* sect. *Implexae* and *Nodobryoria oregana*	48°41.510' N	114°44.173'W	Yes	x	x	
Athelia seborrheica	SG526	outside Stryker, Montana, 6 Apr 2019	1211	S Goyette 635	lichen/ epiphyte	*Bryoria* sect. *Implexae*	48°41.510' N	114°44.173'W	Yes	x		
Athelia seborrheica	SG527	Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 636	lichen/ epiphyte	*Bryoria* sect. *Implexae*	48°40.391' N	115°01.109'W	Yes	x	x	
Athelia seborrheica	SG528	Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 637	lichen/ epiphyte	*Bryoria* sect. *Implexae*	48°40.391' N	115°01.109'W	Yes	x	x	

Athelia seborrheica	SG542	Mukiki Lake, Alberta, 18 May 2019	1580	S Goyette 638	lichen/ ground	*Bryoria*, *Usnea*, and *Hypogymnia*	52°50.678' N	116°51.715'W	No	x	x	
Athelia seborrheica	SG548	Yellowhead County, Alberta, 18 May 2019	1935	S Goyette 639	lichen/ epiphyte	*Bryoria simplicior*, *Bryoria fuscescens*, and *Usnea*	52°53.110' N	116°58.891'W	No	x	x	
Athelia seborrheica	SG556	Coquihalla Pass, British Columbia, 11 May 2019	1220	T Spribille	lichen/ ground	*Alectoria sarmentosa*	49°35'38.2"N	121°07'16.8"W	No	x		
Athelia seborrheica	SG558	Coquihalla Pass, British Columbia, 11 May 2019	1220	T Spribille	lichen/ ground	*Alectoria sarmentosa*	49°35'38.2"N	121°07'16.8"W	No	x	x	
Athelia seborrheica	SG560	north of Rock Island Lake, Alberta, 26 Apr 2019	770	T Spribille	lichen/ ground	*Bryoria, Evernia mesomorpha*, and *Usnea*	55°34.958' N	113°27.010'W	No	x	x	

Athelia seborrheica	SG562	outside of Mukiki Lake, Alberta, 18 May 2019	1935	S Goyette 641	lichen/ ground	*Bryoria* sect. *Implexae*	52°53.110' N	116°58.891'W	No	x		
Athelia seborrheica	SG564	Mukiki Lake, Alberta, 18 May 2019	1580	S Goyette 643	lichen/ ground	*Bryoria* sect. *Implexae* and *Usnea*	52°50.678' N	116°51.715'W	No	x		
Athelia seborrheica	SG567	Lily Lake Trail, Alberta, 25 May 2019	970	T Spribille	lichen/ epiphyte	*Bryoria pikei/ capillaris* and *Usnea*	55°28'01.3 "N	114°42'49 .1"W	No	x		
Athelia seborrheica	SG572	Coquihalla Pass, British Columbia, 11 May 2019	1220	T Spribille	lichen/ epiphyte	*Alectoria*, *Platismatia*, and *Hypogymnia*	49°35'38.2 "N	121°07'16 .8"W	No	x	x	
Athelia seborrheica	SG574	outside Stryker/ Stillwater, Montana, 6 Apr 2019	1211	S Goyette 645	lichen/ epiphyte	NA	48°41.510' N	114°44.173'W	No	x	x	

Athelia seborrheica	SG624	Uppland, Vänge parish, 5.5 km NW of Vänge village, 25 m W of the border to the nature reserve Fiby Urskog, Sweden	130	T Spribille	lichen/ epiphyte	*Bryoria* sect. *Implexae*	59°52'51.7 "N	17°21'05. 9"E	No	x		
Athelia seborrheica	SG635	Little Lost Lake trail loop, British Columbia, 11 May 2019	800	S Goyette 646	lichen/ epiphyte	*Bryoria* sect. *Implexae*	55°36'36.5 "N	114°34'11 .6"W	No	x		
Athelia seborrheica	SG641	Marten Lakes Wilderness Campus, Alberta, 21 Sep 2019	800	S Goyette 648	lichen/ epiphyte	*Usnea*	55°36'35.0 "N	114°33'35 .0"W	Yes	x		
Athelia seborrheica	SG653	Philip Creek drainage: 1 km west of Philip Lake, Upper Clearwater Valley, British Columbia, 28 Aug 2019	1600	T. Goward 19-154	lichen/ epiphyte	*Bryoria glabra*	51°52'15.4 "N	119°55'02 .3"W	No	x		

Athelia seborrheica	SG656	26 km north of Clearwater Village: 1 km w of "Edgewood Blue", Upper Clearwater Valley, British Columbia, 28 Aug 2019	715	T. Goward 19-155	lichen/ epiphyte	*Bryoria* sect. *Implexae*	51°52'09.7"N	120°01'18.0"W	No	x		
Athelia seborrheica	SG588	Hurricane Ridge, Clallam Co., Washington (fallen log), 19 Sep 2014	1645	VS 8747	Wood; fallen log	NA	47°56'01.2"N	123°24'23.2"W	Yes	x		
Athelia aff. seborrheica	SG441	Marten Lakes Wilderness Campus, Alberta, 22 Sep 2018	800	S Goyette 581	lichen/ epiphyte	*Bryoria* sect. *Implexae*	55°36'36.5"N	114°34'11.6"W	No	x		a priori collection and extraction
Athelia aff. seborrheica	SG550	Yellowhead County, Alberta, 18 May 2019	1935	S Goyette 640	lichen/ ground	*Bryoria sect. Implexae* and *Usnea*	52°53.110'N	116°58.891'W	No	x	x	

Athelia acrospora Jülich	8230	Scandinavia		K-H Larsson		NA			No	x		
Athelia acrospora Jülich	SG357	Trophy Mountain, British Columbia, 9 Jun 18	1802	S Goyette 525	lichen/ epiphyte	*Bryoria sect. Implexae*	51°45.611' N	119°56.287'W	No	x		a priori collection and extraction
Athelia acrospora Jülich	SG414	outside Nojack, Alberta, 9 May 18	821	S Goyette 393	lichen/ epiphyte	*Bryoria (subcana) fuscesens*	53°35.070' N	115°37.341'W	No	x		a priori collection and extraction
Athelia acrospora Jülich	SG519	near La Ronge, Saskatchewan, 28 Apr 18	446	T Spribille	lichen/ ground	*Bryoria, Evernia mesomorpha*, and *Usnea*	55°06.987' N	105°15.141'W	No	x		
Athelia acrospora Jülich	SG520	near La Ronge, Saskatchewan, 28 Apr 18	446	T Spribille	lichen/ ground	*Bryoria, Evernia mesomorpha*, and *Usnea*	55°06.987' N	105°15.141'W	No	x		

Athelia acrospora Jülich	SG555	Coquihalla Pass, British Columbia, C, 11 May 2019	1220	T Spribille	lichen/ ground	*Alectoria sarmentosa*	49°35'38.2 "N	121°07'16 .8"W	No	x		
Athelia acrospora Jülich	SG570	outside Lower Goat River Trail, British Columbia,12 May 19	1420	S Goyette 644	lichen/ ground	*Bryoria, Alectoria*, and *Usnea*	53°26'43.0 "N	120°39'21 .0"W	No	x		
Athelia acrospora Jülich	SG573	Coquihalla Pass, British Columbia, 11 May 19	1220	T Spribille	lichen/ ground	*Platismatia*	49°35'38.2 "N	121°07'16 .8"W	No	x		
Athelia acrospora Jülich	SG586	Gypsy Meadows, Pend Oreille Co., Washington 17 Oct 2014	1310	VS 8701a	wood; fallen log	NA	48°54'15.0 "N	117°04'45 .3"W	Yes	x	x	
Athelia arachnoidea (Berk.) Jülich	SG621	Kainbach bei Voitsberg, Austria	1170	T Spribille	lichen/ epiphyte	*Bryoria, Pseudevernia furfuracea*, and *Usnea*	47°10'04.3 "N	14°58'13. 9"E	No	x		

Athelia cf. *arachnoidea*	SG639	in string fen near Lac La Biche, Alberta	690	S Goyette 647	lichen/ ground	*Bryoria fuscescens, Usnea*, and *Hypogymnia*	55°15'19.8 "N	111°18'47 .4"W	No	x		
Group I – Athelia bombacina Pers.	SG563	outside of Mukiki Lake, Alberta, 18 May 19	1935	S Goyette 642	wood	NA	52°53.110' N	116°58.89 1'W	No	x		
Group I – Athelia epiphylla Pers.	SG582	Whitehorse Wildland Provinical Park, Yellowhead Co., Aberta, 26. July 2015	1610	VS 8961	wood	NA	52°59'01.2 "N	117°20'48 .3"W	Yes	x	x	
Group I – Athelia epiphylla Pers.	SG593	Whitehorse Wildland Provinical Park, Yellowhead Co., Aberta, 26. July 2015	1610	VS 8958	wood	NA	52°59'01.2 "N	117°20'48 .3"W	Yes	x	x	
Group I – Athelia epiphylla Pers.	SG615	Small tributary of North Sask River, East of Devon, Alberta, 16 June 1999	680	UA10144	wood	NA	53°21'19.9 "N	113°42'36 .0"W	Yes	x		

Group I – Athelia sp.	SG518	near La Ronge, Saskatchewan, 28 Apr 18	446	T Spribille	lichen/ ground	*Bryoria, Evernia mesomorpha*, and *Usnea*	55°06.987' N	105°15.141'W	No	x	x	
Group II – Athelia cystidiolophora Parm.	SG600	Vazhinka, Podporozhie Dist., Leningrad Reg., Russia,16 Sept 2017	160	VS 11390	wood	NA	61°14'06.8"N	33°52'40.9"E	Yes	x		
Group II – Athelia cystidiolophora Parm.	SG601	Panzelka, Lukoyanov Dist., Nizhny Novgorod Reg., Russia 26 July 2018	70	VS 12063	wood	NA	54°51'38.1"N	44°20'40.6"E	No	x		
Group II – Athelia cystidiolophora Parm.	SG603	Krastelikha, Bogorodsk Dist., Nizhny Novgorod Reg., Russia, 5 Sept 2011	130	VS 4442	wood	NA	56°07'29.3"N	43°27'14.3"E	Yes	x		
Group II – Athelia decipiens s.l. (v. Höhn. et Litsch.) J. Erikss.	SG604	Krastelikha, Bogorodsk Dist., Nizhny Novgorod Reg., Russia, 2 Oct 2015	130	VS 9867	wood	NA	56°07'29.3"N	43°27'14.3"E	Yes	x		

Group II – Athelia decipiens s.l. (v. Höhn. et Litsch.) J. Erikss.	SG610	Sanki, Lukoyanov Dist., Nizhny Novgorod Reg., Russia, 20 Aug 2015	70	VS 9737	wood	NA	54°50'23.3"N	44°13'44.7"E	Yes	x		
Group II – Athelia decipiens (v. Höhn. et Litsch.) J. Erikss.	SG596	Sanki, Lukoyanov Dist., Nizhny Novgorod Reg., Russia, 4 Aug 2017	70	VS 11357	wood	NA	54°50'23.3"N	44°13'44.7"E	Yes	x	x	
Group II – Athelia decipiens (v. Höhn. et Litsch.) J. Erikss.	SG597	Kyvyty, Verkhneburei nskii Dist., Khabarovsk Reg., Russia, 17 Aug 2014	600	VS 7395	wood	NA	50°24'04.6"N	133°13'39.0"E	Yes	x		
Group II – Athelia epiphylla s.l. Pers.	SG595	Chagoda, Boksitogorsk Dist., Leningrad Reg., Russia, 9 May 2018	40	VS 11884	wood	NA	59°08'51.4"N	35°18'42.0"E	Yes	x	x	
Group II – Athelia epiphylla Pers.	SG594	Sanki, Lukoyanov Dist., Nizhny Novgorod Reg., Russia, 20 Aug 2015	70	VS 9719	wood	NA	54°50'23.3"N	44°13'44.7"E	Yes	x		

Table 2 Atheliaceae voucher information from GenBank. When provided, substrate of *Athelia* was acquired from accession data. ITS and EFI-α refer to the GenBank accession numbers per specimen per locus. *Leptosporomyces raunkiaeri* (M.P. Christ) Jülich and *Piloderma fallax* (Lib.) Stalpers were chosen as outgroup taxa.

Species ID	Voucher ID	Substrate	Locality	ITS	EFI-α
Athelia acrospora	UC2022961	wood/ soil	California, USA	KP814228	-
Athelia acrospora	UC2022957	wood/ soil	Oregon, USA	KP814332	-
Athelia acrospora	UC2022976	wood/ soil	Montana, USA	KP814372	-
Athelia acrospora	UC2022956	wood/ soil	Montana, USA	KP814375	-
Athelia acrospora	UC2022960	wood/ soil	Montana, USA	KP814376	-
Athelia arachnoidea	UC2022900	wood/ soil	Montana, USA	KP814459	-
Athelia arachnoidea	CBS:105.18	unknown	Germany	KY025592	-
Athelia arachnoidea	CBS:418.72	unknown	Netherlands	MH860510	GU187672
Athelia bombacina	UC2023122	wood/ soil	Wyoming, USA	KP814299	-
Athelia bombacina	UC2023176	wood/ soil	Idaho, USA	KP814356	-
Athelia bombacina	UC2023189	wood/ soil	Montana, USA	KP814384	-
Athelia bombacina	UC2023159	wood/ soil	Montana, USA	KP814388	-
Athelia bombacina	UC2023173	wood/ soil	Montana, USA	KP814391	-
Athelia decipiens	NFLI 2000-87/10/1	unknown	unknown	JQ358800	
Athelia decipiens	CBS:103869	unknown	Finland	KY025593	-
Athelia decipiens	MO311848	wood	Tennessee, USA	MH558297	-
Athelia decipiens	FCUG 1762	unknown	unknown	U85797	-
Athelia epiphylla	SFC21080314-01	unknown	South Korea	MK992816	-
Athelia epiphylla	CFMR:FP-100564	wood	Maryland, USA	GU187501	GU187676
Athelia arachnoidea	ATCC 10866	unknown	unknown	U85789	-
Leptosporomyces raunkiaeri	CFMR:HHB-7628	wood	Michigan, USA	GU187528	GU187719
Piloderma fallax	CFMR:S-12	unknown	Wisconsin, USA	GU187535	GU187738

Table 3 List of primers used and/ or developed in this study to target *Athelia* internal transcribed spacer region (ITS) and translation elongation factor 1- α (EF1- α) used and/ or developed in this study, as well as host intergenomic spacer (IGS), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), and ITS.

Gene Region	Abbreviation	5' – 3'	Source
ITS (forward)	Ath_ITS_F1	TATAAGGCTYTGATTGTGC	This study
ITS (reverse)	Ath_ITS_R1	AATGGTTTRTAAAATTGTCC	This study
EF1-α (forward)	Ath_EF1a_F4	AYGCYCTSTTGGCGTTCACYC	This study
EF1-α (reverse)	Ath_EF1a_R4	GCGACAGTTTGYCTCATGTCACGG	This study
ITS (forward)	ITS1-F	CTTGGTCATTTAGAGGAAGTAA	Gardes & Bruns (1993)
ITS (reverse)	ITS4	TCCTCCGCTTATTGATATGC	White et al. (1990)
EF1-α (forward)	EF983	GCYCCYGGHCAYCGTGAYTTYAT	Rehner & Buckley (2005)
EF1-α (reverse)	EF2218R	ATGACACCRACRGCRACRGTYTG	Rehner & Buckley (2005)
IGS (forward)	IGS12B	AGTCTGTGGATTAGTGGCCG	Printzen & Ekman (2002)
IGS (reverse)	SSU72R	TTGCTTAAACTTAGACATG	Gargas & Taylor (1992)
GAPDH (forward)	Gpdl-LM	ATTGGCCGCATCGTCTTCCGCAA	Myllys et al. (2002)
GAPDH (reverse)	Gpd2-LM	CCCACTCGTTGTCGTACCA	Myllys et al. (2002)

Table 4 Voucher information for *Bryoria* sect. *Implexae* ITS, IGS, and GAPDH sequences from GenBank. ITS, IGS, and GAPDH refer to the GenBank accession numbers per specimen per locus.

Genus species	Voucher ID	Source	ITS	IGS	GAPDH
Bryoria capillaris (Ach.) Brodo & D. Hawksw.	L141	Velmala et al., 2014	FJ668493	FJ668455	FJ668399
Bryoria capillaris (Ach.) Brodo & D. Hawksw.	L211	Velmala et al., 2014	GQ996287	KJ396487	GQ996259
Bryoria capillaris (Ach.) Brodo & D. Hawksw.	L270	Velmala et al., 2014	GQ996288	KJ396488	GQ996260
Bryoria capillaris (Ach.) Brodo & D. Hawksw.	S192	Velmala et al., 2014	GQ996289	KJ396490	GQ996261
Bryoria capillaris (Ach.) Brodo & D. Hawksw.	S2	Velmala et al., 2014	KJ396433	KJ396489	KJ954306
Bryoria friabilis Brodo & D. Hawksw.	L407	Velmala et al., 2014	KJ396435	KJ396492	KJ954308
Bryoria friabilis Brodo & D. Hawksw.	S395a	Velmala et al., 2014	KJ576728	KJ396493	KJ599481
Bryoria friabilis Brodo & D. Hawksw.	L355	Velmala et al., 2014	KJ396434	KJ396491	KJ954307
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S260b	Velmala et al., 2014	GQ996286	KJ396508	GQ996258
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L149	Velmala et al., 2014	GQ996290	KJ396496	GQ996262
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S56	Velmala et al., 2014	GQ996291	KJ396502	GQ996263
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L160	Velmala et al., 2014	GQ996300	KJ396497	GQ996272
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S274	Velmala et al., 2014	GQ996303	KJ396512	GQ996276
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L232	Velmala et al., 2014	GQ996304	KJ396500	GQ996277
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L189	Velmala et al., 2014	GQ996305	KJ396498	GQ996278
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S157	Velmala et al., 2014	GQ996306	KJ396504	GQ996279

Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S256	Velmala et al., 2014	GQ996307	KJ396505	GQ996280
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L139	Velmala et al., 2014	KJ396436	KJ396495	KJ954309
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L224	Velmala et al., 2014	KJ396437	KJ396499	KJ954310
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L305	Velmala et al., 2014	KJ396438	–	–
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	L307	Velmala et al., 2014	KJ396439	–	KJ954311
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S109	Velmala et al., 2014	KJ396440	KJ396503	KJ954312
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S259	Velmala et al., 2014	KJ396441	KJ396506	KJ954313
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S260a	Velmala et al., 2014	KJ396442	KJ396507	KJ954314
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S261	Velmala et al., 2014	KJ396443	KJ396509	KJ954315
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S369	Velmala et al., 2014	KJ396444	KJ396514	KJ954316
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S379	Velmala et al., 2014	KJ396445	KJ396515	KJ954317
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S380	Velmala et al., 2014	KJ396446	KJ396516	KJ954318
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S24	Velmala et al., 2014	KJ576715	KJ396501	KJ599468
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S267	Velmala et al., 2014	KJ576716	KJ396510	KJ599469
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S272	Velmala et al., 2014	KJ576717	KJ396511	KJ599470
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	S277a	Velmala et al., 2014	KJ576718	KJ396513	KJ599471
Bryoria glabra (Motyka) Brodo & D. Hawksw.	L186	Velmala et al., 2014	FJ668494	FJ668456	FJ668400
Bryoria implexa (Hoffmann) Brodo & D. Hawksw	S22	Velmala et al., 2014	GQ996294	KJ396517	GQ996266

Bryoria implexa (Hoffmann) Brodo & D. Hawksw	S67	Velmala et al., 2014	KJ396447	KJ396520	KJ954319
Bryoria implexa (Hoffmann) Brodo & D. Hawksw	S168	Velmala et al., 2014	KJ396448	KJ396521	KJ954320
Bryoria implexa (Hoffmann) Brodo & D. Hawksw	S36	Velmala et al., 2014	KJ576719	KJ396518	KJ599472
Bryoria implexa (Hoffmann) Brodo & D. Hawksw.	S39	Velmala et al., 2014	GQ996293	KJ396519	GQ996265
Bryoria inactiva Goward, Velmala, & Myllys	L206	Velmala et al., 2014	GQ996283	KJ396522	GQ996255
Bryoria inactiva Goward, Velmala, & Myllys	S239a	Velmala et al., 2014	GQ996284	KJ396526	GQ996256
Bryoria inactiva Goward, Velmala, & Myllys	L323b	Velmala et al., 2014	KJ396449	KJ396523	KJ954321
Bryoria inactiva Goward, Velmala, & Myllys	L347	Velmala et al., 2014	KJ396450	KJ396524	KJ954322
Bryoria inactiva Goward, Velmala, & Myllys	L358	Velmala et al., 2014	KJ396451	KJ396525	KJ954323
Bryoria inactiva Goward, Velmala, & Myllys	S392a	Velmala et al., 2014	KJ396452	KJ396528	KJ954324
Bryoria kockiana Velmala, Myllys & Goward	L394	Velmala et al., 2014	KJ396453	KJ396529	KJ954325
Bryoria kockiana Velmala, Myllys & Goward	L396	Velmala et al., 2014	KJ396454	KJ396530	KJ954326
Bryoria kuemmerleana (Gyeln.) Brodo & D. Hawksw.	L244a	Velmala et al., 2014	GQ996295	KJ396531	GQ996267
Bryoria kuemmerleana (Gyeln.) Brodo & D. Hawksw.	L274	Velmala et al., 2014	GQ996296	KJ396532	GQ996268
Bryoria kuemmerleana (Gyeln.) Brodo & D. Hawksw.	L275	Velmala et al., 2014	KJ396455	KJ396533	KJ954327
Bryoria kuemmerleana (Gyeln.) Brodo & D. Hawksw.	S160	Velmala et al., 2014	KJ396456	KJ396535	KJ954328
Bryoria kuemmerleana	S128	Velmala et al., 2014	KJ576720	KJ396534	KJ599473

(Gyeln.) Brodo & D. Hawksw.					
Bryoria pikei Brodo & D. Hawksw.	L209	Velmala et al., 2014	GQ996281	KJ396538	GQ996253
Bryoria pikei Brodo & D. Hawksw.	L197	Velmala et al., 2014	KJ396457	KJ396536	KJ954329
Bryoria pikei Brodo & D. Hawksw.	L200	Velmala et al., 2014	KJ396458	KJ396537	KJ954330
Bryoria pikei Brodo & D. Hawksw.	L374	Velmala et al., 2014	KJ396459	KJ396540	KJ954331
Bryoria pikei Brodo & D. Hawksw.	L376	Velmala et al., 2014	KJ396460	KJ396541	KJ954332
Bryoria pikei Brodo & D. Hawksw.	L377	Velmala et al., 2014	KJ396461	KJ396542	KJ954333
Bryoria pikei Brodo & D. Hawksw.	L421	Velmala et al., 2014	KJ396462	KJ396543	KJ954334
Bryoria pikei Brodo & D. Hawksw.	S221	Velmala et al., 2014	KJ396463	KJ396544	KJ954335
Bryoria pikei Brodo & D. Hawksw.	S362	Velmala et al., 2014	KJ396464	KJ396545	KJ954336
Bryoria pikei Brodo & D. Hawksw.	S368	Velmala et al., 2014	KJ396465	KJ396546	KJ954337
Bryoria pikei Brodo & D. Hawksw.	S382	Velmala et al., 2014	KJ396466	KJ396547	KJ954338
Bryoria pikei Brodo & D. Hawksw.	S383a	Velmala et al., 2014	KJ396467	KJ396548	KJ954339
Bryoria pikei Brodo & D. Hawksw.	S390	Velmala et al., 2014	KJ396468	KJ396549	KJ954340
Bryoria pikei Brodo & D. Hawksw.	L210	Velmala et al., 2014	KJ576714	KJ396539	KJ599467
Bryoria pikei Brodo & D. Hawksw.	S394	Velmala et al., 2014	KJ576727	KJ396550	KJ599480
Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.	S222	Velmala et al., 2014	KJ396469	KJ396551	KJ954341
Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.	S232	Velmala et al., 2014	KJ396470	KJ396552	KJ954342
Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.	S370	Velmala et al., 2014	KJ396471	KJ396553	KJ954343
Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.	S371	Velmala et al., 2014	KJ396472	KJ396554	KJ954344
Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.	S377	Velmala et al., 2014	KJ396473	KJ396555	KJ954345

Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.	S386	Velmala et al., 2014	KJ576725	KJ396556	KJ599478
Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw.	S387	Velmala et al., 2014	KJ576726	KJ396557	KJ599477
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S164	Velmala et al., 2014	GQ996285	KJ396574	GQ996257
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S10	Velmala et al., 2014	GQ996297	KJ396564	GQ996269
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S32	Velmala et al., 2014	GQ996298	KJ396565	GQ996270
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	L272	Velmala et al., 2014	GQ996299	KJ396558	GQ996271
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	L300	Velmala et al., 2014	GQ996301	KJ396562	GQ996274
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S45	Velmala et al., 2014	GQ996302	KJ396568	GQ996275
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S166	Velmala et al., 2014	GQ996308	KJ396575	GQ996273
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	L273	Velmala et al., 2014	KJ396474	KJ396559	KJ954346
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	L279	Velmala et al., 2014	KJ396475	KJ396560	KJ954347
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	L286	Velmala et al., 2014	KJ396476	KJ396561	KJ954348
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S6	Velmala et al., 2014	KJ396477	KJ396563	KJ954349
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S42	Velmala et al., 2014	KJ396478	KJ396566	KJ954350
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S43	Velmala et al., 2014	KJ396479	KJ396567	KJ954351
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S59	Velmala et al., 2014	KJ396480	KJ396571	KJ954352
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S72	Velmala et al., 2014	KJ396481	KJ396573	KJ954353
Bryoria vrangiana	S196	Velmala et al., 2014	KJ396482	KJ396576	KJ954354

(Gyeln.) Brodo & D. Hawksw.					
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S341b	Velmala et al., 2014	KJ396483	KJ396577	KJ954355
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S385	Velmala et al., 2014	KJ396484	KJ396578	KJ954356
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S62	Velmala et al., 2014	KJ576721	KJ396572	KJ599474
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S57	Velmala et al., 2014	KJ576722	KJ396570	KJ599475
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S47	Velmala et al., 2014	KJ576723	KJ396569	KJ599476
Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw.	S396	Velmala et al., 2014	KJ576729	KJ396579	KJ599482
Bryoria sp.	L392	Velmala et al., 2014	KJ396485	KJ396580	KJ954357
Bryoria sp.	L395	Velmala et al., 2014	KJ396486	KJ396581	KJ954358

Table 5 Best partitioning scheme for each locus in the concatenated *Athelia* alignment. Results of the *Athelia* gene partitioning scheme and model selection indicate that ITS and each codon of EF1-α should run with separate evolutionary models during the maximum likelihood tree search..

Selection parameters – Branch lengths: linked; Models: GTR, GTR+G, GTR_I_G; Model Selection: AICc; Search: user defined. Scheme: all_separate; Scheme lnL: -7994.59130859375; Scheme AICc: 16470.161797; Parameters: 212; Sites: 1798; Subsets: 4; Scheme_all_separate (ITS) (EF1a_1) (EF1a_2) (EF1a_3).

Subset	Best Model	# sites	subset id	Partition names
1	GTR+G	715	10f75124a16cf7d37c17fe8956bcfcf7	ITS
2	GTR+G	361	b187892c48de77297196ce6c9038c24f	EF1a_1
3	GTR+G	361	97a7a71dc9d02763592bcb81a2dbfac9	EF1a_2
4	GTR+G	361	40f0c33692ebd309f12d1f77fad3cdc3	EF1a_3

Table 6 Best partitioning scheme for each locus in the concatenated *Bryoria* sect. *Implexae* alignment. Results of the *Bryoria* sect. *Implexae* gene partitioning scheme and model selection show that ITS, IGS, and each codon of GAPDH should run with separate evolutionary models during the maximum likelihood tree search.

Selection parameters – Branch lengths: linked; Models: GTR, GTR+G, GTR_I_G; Model Selection: AICc; Search: user defined. Scheme: all_separate; Scheme lnL: -4533.428771972656; Scheme AICc: 9833.5784879; Parameters: 322; Sites: 2018; Subsets: 5; Scheme_all_separate (ITS) (IGS) (GAPDH_1) (GAPDH_2) (GAPDH_3).

Subset	Best Model	# sites	subset id	Partition names
1	GTR+G	543	07eb0ebcb45476a9ba30b7a0227ebc21	ITS
2	GTR+G	421	e00bfb2dbbbeb0272d05757e5ecdd01c	IGS
3	GTR+G	352	e7fb4407e52cdf0ad0e4f50a945adde7	GAPDH_1
4	GTR	351	f81b7afb4a378d97cb7fbfea865e5574	GAPDH_2
5	GTR	351	0da36c06d84bdad41286d26d2fa6cc4b	GAPDH_3

Table 7 Approximately Unbiased (AU) test results suggest substrate preference does not explain evoluationary relationships across.

Constr.: constrained tree.
deltaL : logL difference from the maximal logL in the set.
p-AU : p-value of approximately unbiased (AU) test (Shimodaira, 2002).

Plus signs denote the 95% confidence sets.
Minus signs denote significant exclusion.
All tests performed 10000 resamplings using the RELL method.

Tree	**logL**	**deltaL**	**p-AU**
Tree 1: unconstrained (original) concatenated *Athelia* ML tree	-8048.089	0	0.9798+
Constr. 1: *Athelia* associated with epiphytic lichens are reciprocally monophyletic	-8746.805	698.716	0.0027-
Constr. 2: *Athelia* associated with fallen lichens are reciprocally monophyletic	-8760.701	712.613	0.0304-
Constr. 3: *Athelia* associated with wood or soil are reciprocally monophyletic	-8775.245	727.156	0-

Table 8 Average pairwise distance of ITS sequences between and within-strata of *Athelia* species/ group haplotypes. Results suggest greater nucleotide variation across members of *Athelia* than within *Athelia seborrheica.*

WITHIN		
stratum	***mean***	
acrospora	0.04131185	
arachnoidea	0.04810127	
Group I	0.03066104	
Group II	0.01821378	
seborrhea	0.02000817	
BETWEEN		
strata.1	***strata.2***	***mean***
acrospora	arachnoidea	0.04856157
acrospora	Group I	0.03607595
acrospora	Group II	0.0344649
acrospora	seborrheica	0.03525065
arachnoidea	Group I	0.05518987
arachnoidea	Group II	0.04189873
arachnoidea	seborrheica	0.04392801
Group I	Group II	0.03753165
Group I	seborrheica	0.03748022
Group II	seborrheica	0.01863133

Table 9 Average pairwise distance of EFI-α sequences between and within-strata of *Athelia* species/ group haplotypes. Results suggest greater nucleotide variation across members of *Athelia* than within *Athelia seborrheica.*

WITHIN		
stratum	***mean***	
Group I	0.13035382	
Group II	0.03910615	
seborrheica	0.01912801	
BETWEEN		
strata.1	***strata.2***	***mean***
Group I	Group II	0.12274984
Group I	seborrheica	0.07159761
Group II	seborrheica	0.08715472

Table 10 Results from the one-way analysis of variance (ANOVA) of morphological measurements between different species of *Athelia*. There are significant differences between basidia length and width, sterigmata length and width, and basidiospore length and width, but not in hyphal diameter for the species measured. Significant P-values are bolded and indicated by ***.

basidium.width~species_group

	Df	Sum_Sq	Mean_Sq	F_value	Pr(>F)
species_group	3	53.39	17.798	44.17	**<2e-16*** **
Residuals	326	131.34	0.403		

spore.width~species_group

	Df	Sum_Sq	Mean_Sq	F_value	Pr(>F)
species_group	3	22.27	7.425	26.14	**3.56e-15*** **
Residuals	326	92.61	0.284		

sterigmata.width~species_group

	Df	Sum_Sq	Mean_Sq	F_value	Pr(>F)
species_group	3	0.55	0.1817	1.689	0.169
Residuals	325	34.96	0.1076		

hyphal.diameter~species_group

	Df	Sum_Sq	Mean_Sq	F_value	Pr(>F)
species_group	3	8.53	2.8437	7.518	**7.11e-05*** **
Residuals	316	119.53	0.3782		

basidum.length~species_group

	Df	Sum_Sq	Mean_Sq	F_value	Pr(>F)
species_group	3	1357	452.4	76.28	**<2e-16*** **
Residuals	326	1934	5.9		

spore.length~species_group

	Df	Sum_Sq	Mean_Sq	F_value	Pr(>F)
species_group	3	38.91	12.97	20.32	**4.28e-12*** **
Residuals	326	208.11	0.638		

sterigmata.length~species_group

	Df	Sum_Sq	Mean_Sq	F_value	Pr(>F)
species_group	3	135.5	45.16	26.45	**2.45e-15*** **
Residuals	326	556.6	1.71		

Table 11 Identity and frequency count of lichen hosts infected by *Athelia*. The genus *Bryoria* appears to be the preferential host genus, with species in *Bryoria* section *Implexae* most frequently encountered out of all macrolichens surveyed. All belong to the family Parmeliaceae.

Lichen Host	**Specimen Count**
Bryoria sect. *Implexae* (Gyeln.) Brodo & D. Hawksw.	42
Bryoria fremontii (Tuck.) Brodo & D.	3
Bryoria tortuosa (G. Merr.) Brodo & D. Hawksw.	1
Bryoria simplicior (Vain.) Brodo & D. Hawksw.	1
Bryoria sp. Brodo & D. Hawks.	8
Alectoria sarmentosa (Ach.) Ach.	5
Nodobryoria abbreviata (Müll. Arg.) Common & Brodo	1
Nodobryoria oregana (Tuck. ex Nyl.) Common & Brodo	2
Usnea spp.	16
Evernia mesomorpha Nyl.	3
Hypogymnia physodes (L.) Nyl.	4
Platismatia glauca (L.) W.L. Culb. & C.F. Culb.	2

Table 12 Voucher information for *Bryoria* sect. *Implexae* (Gyeln.) Brodo and D. Hawksw. collected and sequenced for this study. Final GenBank accession numbers for ITS, IGS, and GAPDH will be obtained upon formal submission of the publication. Successfully sequenced loci are indicated with an "x".

Genus species	Extraction number	Locality	Elevation (m)	Collection number	Latitude	Longitude	ITS	IGS	GAPDH
Bryoria sect. Implexae	SG357	Trophy Mountain, British Columbia, 9 Jun 2018	1802	S Goyette 525	51°45.611'N	119°56.287'W		x	x
Bryoria sect. Implexae (pikei)	SG410	~1-1.5 km from HWY to Fort McMurray (backroad), Alberta, 20 Apr 2018	592	S Goyette 299	55°23.596'N	112°28.396'W		x	x
Bryoria sect. Implexae (subcana)	SG414	outside Nojack, Alberta, 9 May 2018	821	S Goyette 393	53°35.070'N	115°37.341'W		x	x
Bryoria sect. Implexae (capillaris)	SG426	Athabasca County, Alberta, 4 Jun 2018	539	S Goyette 522	54°57.056'N	112°57.280'W		x	x
Bryoria sect. Implexae	SG436.1	Marten Lakes Wilderness Campus, Alberta, 23 Sep 2018	800	S Goyette 583	55°36'35.0"N	114°33'35.0"W	x	x	x
Bryoria sect. Implexae (capillaris)	SG441	Marten Lakes Wilderness Campus, Alberta, 22 Sep 2018	800	S Goyette 581	55°36'36.5"N	114°34'11.6"W		x	

Bryoria sect. Implexae (subcana)	SG441.2	Marten Lakes Wilderness Campus, Alberta, 22 Sep 2018	800	S Goyette 581	55°36'36.5"N	114°34'11.6"W		x	
Bryoria sect. Implexae (fuscescens)	SG450	off HWY 43 before Whitecourt, Alberta, 10 Jul 2018	700	S Goyette 536	54°06'16.5"N	115°37'39.0"W		x	x
Bryoria sect. Implexae (fuscescens)	SG455.1	outside Chinook Cove, British Columbia	760	T Spribille	51°15'31.2"N	120°12'44.7"W		x	x
Bryoria sect. Implexae (capillaris)	SG455.2	outside Chinook Cove, British Columbia	760	T Spribille	51°15'31.2"N	120°12'44.7"W		x	x
Bryoria sect. Implexae (capillaris)	SG456.2	past Falkland, British Columbia	810	T Spribille	50°26'08.4"N	119°30'17.7"W		x	x
Bryoria sect. Implexae (sorediate)	SG458.1	past Falkland, British Columbia	810	T Spribille	50°26'08.4"N	119°30'17.7"W		x	x
Bryoria sect. Implexae (fuscescens)	SG458.3	past Falkland, British Columbia	810	T Spribille	50°26'08.4"N	119°30'17.7"W	x	x	x
Bryoria sect. Implexae (capillaris)	SG458.4	past Falkland, British Columbia	810	T Spribille	50°26'08.4"N	119°30'17.7"W	x	x	x
Bryoria sect. Implexae (fuscescens)	SG459.1	outside Chinook Cove, British Columbia	760	T Spribille	51°15'31.2"N	120°12'44.7"W	x	x	x
Bryoria sect. Implexae (sorediate)	SG459.2	outside Chinook Cove, British Columbia	760	T Spribille	51°15'31.2"N	120°12'44.7"W	x	x	x
Bryoria sect. Implexae (capillaris)	SG459.3	outside Chinook Cove, British Columbia	760	T Spribille	51°15'31.2"N	120°12'44.7"W	x	x	x

Bryoria sect. Implexae (fuscescens)	SG460.1	past Falkland, British Columbia	760	T Spribille	51°15'31.2"N	120°12'44.7"W	x	x	x
Bryoria sect. Implexae (capillaris)	SG460.2	past Falkland, British Columbia	810	T Spribille	51°15'31.2"N	120°12'44.7"W		x	x
Bryoria sect. Implexae	SG461.2	outside Chinook Cove, British Columbia	810	T Spribille	50°26'08.4"N	119°30'17.7"W	x	x	x
Bryoria sect. Implexae (fuscescens)	SG498.2	outside of Lolo Pass, Idaho	1280	S Goyette 626	46°47'05.7"N	114°23'02.1"W	x	x	x
Bryoria sect. Implexae (fuscescens)	SG507.2	outside Stryker, Montana, 6 Apr 2019	1211	S Goyette 629	48°41.510'N	114°44.173'W	x	x	x
Bryoria sect. Implexae (capillaris)	SG507.3	outside Stryker, Montana, 6 Apr 2019	1211	S Goyette 629	48°41.510'N	114°44.173'W	x	x	x
Bryoria sect. Implexae (sorediate)	SG510.1	outside of Stryker, Montana, 6 Apr 2019	1211	S Goyette 630	48°41.510'N	114°44.173'W	x	x	x
Bryoria sect. Implexae (fuscescens)	SG510.2	outside of Stryker, Montana, 6 Apr 2019	1211	S Goyette 630	48°41.510'N	114°44.173'W	x	x	
Bryoria sect. Implexae	SG512.1	Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 631	48°40.391'N	115°01.109'W		x	x
Bryoria sect. Implexae	SG521.2	outside Edna Creek Rd. area, Montana, 7 Apr 2019	446	T Spribille	48°40.391'N	115°01.109'W	x	x	x
Bryoria sect. Implexae	SG524.1	on *Abies lasiocarpa*, Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 633	48°40.391'N	115°01.109'W	x	x	x

Bryoria sect. Implexae (capillaris)	SG524.2	on *Abies lasiocarpa*, Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 633	48°40.391'N	115°01.109'W	x	x	x
Bryoria sect. Implexae (sorediate)	SG525.1	outside Edna Creek Rd. area, Montana, 6 Apr 2019	1211	S Goyette 634	48°41.510'N	114°44.173'W		x	x
Bryoria sect. Implexae (fuscescens)	SG525.2	outside Edna Creek Rd. area, Montana, 6 Apr 2019	1211	S Goyette 634	48°41.510'N	114°44.173'W		x	x
Bryoria sect. Implexae (sorediate)	SG527.1	Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 636	48°40.391'N	115°01.109'W	x	x	x
Bryoria sect. Implexae (capillaris)	SG527.2	Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 636	48°40.391'N	115°01.109'W	x	x	x
Bryoria sect. Implexae (capillaris)	SG528.1	Edna Creek Rd. area, Montana, 7 Apr 2019	1352	S Goyette 637	48°40.391'N	115°01.109'W	x	x	x
Bryoria sp.	SG542.2	Mukiki Lake, Alberta, 18 May 2019	1580	S Goyette 638	52°50.678'N	116°51.715'W	x	x	x
Bryoria sect. Implexae	SG548.1	Yellowhead County, Alberta, 18 May 2019	1935	S Goyette 639	52°53.110'N	116°58.891'W	x	x	x
Bryoria sp.	SG548.3	Yellowhead County, Alberta, 18 May 2019	1935	S Goyette 639	52°53.110'N	116°58.891'W	x	x	x
Bryoria sect. Implexae	SG558.2	Coquihalla Pass, British Columbia, 11 May 2019	1220	T Spribille	49°35'38.2"N	121°07'16.8"W	x		x
Bryoria sect. Implexae	SG567.1	Lily Lake Trail, Alberta, 25 May 2019	970	T Spribille	55°28'01.3"N	114°42'49.1"W		x	x

Bryoria sect. Implexae (fuscescens)	SG574.1	outside Stryker/ Stillwater, Montana, 6 Apr 2019	1211	S Goyette 645	48°41.510'N	114°44.173'W		x	x
Bryoria sect. Implexae	SG624.1	Uppland, Vänge parish, 5.5 km NW of Vänge village, 25 m W of the border to the nature reserve Fiby Urskog, Sweden	130	T Spribille	59°52'51.7"N	17°21'05.9"E		x	x
Bryoria sect. Implexae (pikei)	SG635.2	Little Lost Lake trail loop, British Columbia, 11 May 2019	800	S Goyette 646	55°36'36.5"N	114°34'11.6"W		x	x
Bryoria glabra	SG653.1	Philip Creek drainage: 1 km west of Philip Lake, Upper Clearwater Valley, British Columbia, 28 Aug 2019	1600	T. Goward 19-154	51°52'15.4"N	119°55'02.3"W		x	x
Bryoria sect. Implexae	SG656.1	26 km north of Clearwater Village: 1 km w of "Edgewood Blue", Upper Clearwater Valley, British Columbia, 28 Aug 2019	715	T. Goward 19-155	51°52'09.7"N	120°01'18.0"W		x	x

Table 13 Chemical and morphological data matrix for *Bryoria* sect. *Implexae* following Velmala et al. (2014). Isolates SG512.1 and SG521.2 did not have enough usable material for morphological character scoring or chemical analysis. Isolates SG436.1, SG441.2, SG455.2, SG525.1, and SG574.1 did not have enough usable material for chemical analysis. The "-" indicate that a given character was not present to be scored. For instance if the specimen lacked "pseudocyphellae" subsequent pseudocyphellae characters (color, surface, etc.) could not be included in the data matrix.

1 -orcinol depsidones: absent (0), present (1), see characters 2–4; 2 Fumarprotocetraric acid: absent (0), present only in soralia (1), present in thallus (2); 3 Norstictic acid: absent (0), present (1); 4 Psoromic acid: absent (0), present (1); 5 -orcinol depsides: absent (0), present (1), see characters 6–8; 6 Atranorin and/or chloroatranorin: absent (0), present (1); 7 Alectorialic acid: absent (0), present (1); 8 Barbatolic acid: absent (0), present (1); 9 Gyrophoric acid (= orcinol depside): absent (0), present (1); 10 Soralia: absent (0), present (1); 11 Pseudocyphellae: absent or very rare (0), present (1); 12 Pseudocyphellae color: brownish white (0), white (1); 13 Pseudocyphellae surface: slightly depressed or plane (0), partly raised (1); 14 Pseudocyphellae shape: linear (0), elongate-fusiform (1); 15 Thallus color: gray to pale brown (0), brown (1), dark brown to black (2); 16 Apothecia: absent (0), present (1); 17 Branching angles: mainly acute (0), mainly obtuse (1), both (2); 18 Origin: North America (0), Europe or Asia (1)

	Character																	
Isolate	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
L141	0	0	0	0	1	0	1	1	0	0	0	-	-	-	0	0	2	1
L211	1	1	0	0	1	0	1	1	0	1	0	-	-	-	0	0	0	1
L270	0	0	0	0	1	-	-	1	0	1	0	-	-	-	0	0	0	1
S2	0	0	0	0	1	0	1	1	0	1	0	-	-	-	0	0	0	1
S192	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1
L355	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0	2	0
L407	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	2	0
L395a	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	-	1	0
L147	1	2	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	1
L139	1	2	0	0	0	0	0	0	0	1	0	-	-	-	0	0	0	1
L149	1	2	0	0	0	0	0	0	0	1	0	-	-	-	1	0	0	1
L160	1	2	0	0	1	1	0	0	0	1	0	-	-	-	1	0	0	1
L189	1	2	0	0	0	0	0	0	0	1	0	-	-	-	0	0	0	1
L224	1	2	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	1
L232	1	1	0	0	1	1	0	0	0	1	0	-	-	-	2	0	2	1
S24	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	1
S56	1	2	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	1
S109	1	2	0	0	1	1	0	0	0	1	0	-	-	-	0	0	0	1
S157	1	2	0	0	1	1	0	0	0	1	0	-	-	-	1	0	2	1
S256	1	1	0	0	0	0	0	0	0	1	0	-	-	-	1	0	0	0
S259	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0

S260a	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0
S260b	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0
S261	1	1	0	0	0	0	0	0	0	1	0	-	-	-	1	0	0	0
S267	1	1	0	0	0	0	0	0	0	1	0	-	-	-	1	0	0	0
S272	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0
S274	0	0	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0
S277a	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0
S369	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0
S379	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	0	0
S380	1	1	0	0	0	0	0	0	0	1	-	-	-	-	2	0	0	0
L186	1	1	0	0	0	0	0	0	0	1	0	-	-	-	1	0	2	1
S22	1	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	2	1
S36	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1
S39	1	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1
S67	1	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	2	1
S168	1	0	0	1	1	1	0	0	0	1	1	-	-	-	1	1	0	1
L206	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
L323b	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	0
L347	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	2	0
L358	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0
S239a	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0
S384	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0
S392a	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
L394	1	0	0	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0
L396	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0
L244a	1	0	1	0	1	1	0	0	0	1	1	0	0	1	2	0	0	1
L274	1	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	1
L275	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	0	1	1
S128	1	0	1	0	1	1	1	0	0	0	1	1	0	0	1	0	2	1
S160	1	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	1
L197	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
L200	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
L209	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
L210	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	0	2	0
L374	0	0	0	0	1	0	1	0	1	0	1	0	0	1	2	0	0	0
L376	0	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	0	0
L377	0	0	0	0	1	0	1	0	1	0	1	1	0	1	0	1	2	0
L421	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	0
S221	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0
S362	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0

S368	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
S382	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0
S383a	0	0	0	0	1	0	1	1	0	0	1	1	0	1	0	0	0	0
S390	0	0	0	0	1	0	1	1	0	0	1	-	-	-	1	0	0	0
S394	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0
S222	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
S232	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
S370	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
S371	1	0	1	0	0	0	0	0	0	0	1	1	0	1	2	0	0	0
S377	1	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0
S386	1	0	1	0	0	0	0	0	0	0	1	1	0	1	2	0	0	0
S387	1	0	1	0	0	0	0	0	0	0	1	1	0	1	2	1	2	0
L272	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
L273	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	2	1
L279	1	2	0	0	0	0	0	0	0	1	1	0	0	1	1	0	2	1
L286	1	2	0	0	1	1	0	0	0	1	1	0	0	1	1	1	1	1
L300	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1
S6	1	2	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1
S10	0	0	0	0	0	0	0	0	1	0	1	0	0	-	1	0	2	1
S32	1	1	0	0	1	1	0	0	1	1	1	0	0	1	2	0	0	1
S42	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	1	2	1
S43	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	2	1
S45	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	2	1
S47	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1
S57	1	2	0	0	1	1	0	0	0	0	1	0	0	1	1	1	2	1
S59	1	1	0	0	1	1	0	0	0	1	1	0	0	1	1	0	2	1
S62	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1
S72	1	1	0	0	0	0	0	0	0	1	1	0	0	0	2	0	1	1
S164	1	1	0	0	1	1	0	0	0	1	1	0	0	1	2	0	0	1
S166	1	2	0	0	1	1	0	0	0	1	1	0	0	1	1	0	0	1
S196	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1
S341b	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1
S385	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	2	0
S396	1	2	0	0	1	1	0	0	0	1	1	0	0	1	1	1	0	1
L392	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
L395	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0
SG357	1	0	0	1	1	0	0	1	0	0	0	-	-	-	0	0	0	0
SG410	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0
SG414	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
SG426	1	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0

SG436.1										0	0	-	-	-	2	0	0	0
SG441	1	0	1	0	1	0	0	1	0	1	1	0	0	1	0	0	1	1
SG441.2										1	1	0	0	1	1	0	0	1
SG450	1	1	0	0	0	0	0	0	0	1	1	0	0	0	2	0	0	0
SG455.1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0
SG455.2										0	1	0	0	1	0	0	0	0
SG456.2	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0
SG458.1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	0	2	0
SG458.3	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	2	0
SG458.4	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0
SG459.1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
SG459.2	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0
SG459.3	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0
SG460.1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0
SG460.2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
SG461.2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	2	0
SG498.2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
SG507.2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0
SG507.3	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0
SG510.1	1	1	0	0	0	0	0	0	0	1	0	-	-	-	1	0	1	0
SG510.2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
SG512.1																		0
SG521.2																		0
SG524.1	1	1	0	0	0	0	0	0	0	1	0	-	-	-	0	0	0	0
SG524.2	1	0	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	0
SG525.1										1	1	1	0	1	1	0	2	0
SG525.2	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	2	0
SG527.1	1	1	0	0	0	0	0	0	0	1	0	-	-	-	0	0	1	0
SG527.2	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
SG528.1	1	0	0	1	1	0	0	1	0	0	0	-	-	-	0	0	0	0
SG548.1	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	1	0
SG558.2	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0
SG567.1	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0
SG574.1										1	1	0	0	1	1	0	0	0
SG624.1	1	0	0	1	1	0	0	1	0	0	0	-	-	-	0	0	2	1
SG635.2	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	2	0
SG653.1	1	1	0	0	0	0	0	0	0	1	0	-	-	-	2	0	1	0
SG656.1	1	0	0	1	1	0	0	1	0	0	0	-	-	-	1	1	0	0

Table 14 Diagnostic characters for *Athelia* species most similar to *A. seborrheica*. *Athelia seborrheica* can be differentiated from *A. arachnoidea* in its shorter basidia and four sterigmata, from *A. acrospora* in its stouter basidiospores, and from *A. epiphylla* in its slightly longer though narrower basidia, wider basidiospores, and preferential infection of hair lichens in Parmeliaceae.

Genus species	Basidium length x width (µm)	Sterigmata length x width (µm)	Sterigmata number	Basidiospore length x width width (µm)	Substrate	Reference
Athelia seborrheica	14–18.5–(20) x 5.5–6–(7)	3.5–5.5 x 1–1.5	4, rarely 2	4.5–5.5 x 3–3.5–(4.5)	*Abies lasiocarpa* wood; Lichen: *Bryoria* sect. *Implexae*, *Bryoria fremontii, Bryoria tortuosa, Alectoria sarmentosa, Nodobryoria abbreviata, Nodobryoria oregana, Usnea spp., Evernia mesomorpha, Hypogymnia physodes, Platismatia glauca*	This study
Athelia acrospora	12–15 x 5–6	3 x 8	4, rarely 2	5.5–7–(8) x 2.2–2.6	Gymnosperm and angiosperm wood; Angiosperm leaves	Jülich, 1972
Athelia arachnoidea	24–33 x 6.5–8	5–6 x 1.5–2	2, rarely 4	(7)–8–11–(12) x (3.5)–4–5.5–(6)	Gymnosperm and angiosperm wood; Lichen: *Lecanora* spp., *Physcia ascendens, Xanthoria parietina, Usnea barbata*	Jülich, 1972
Athelia epiphylla	13–15–18 x 5–7–8	4–5 x 1	4, rarely 2	(5.5)–6–7.5–(8) x 2.8–3.2	Gymnosperm and angiosperm wood; various ferns; Moss: *Hylocomium splendens;* Lichen: *Parmelia*, *Xanthoria*	Jülich, 1972

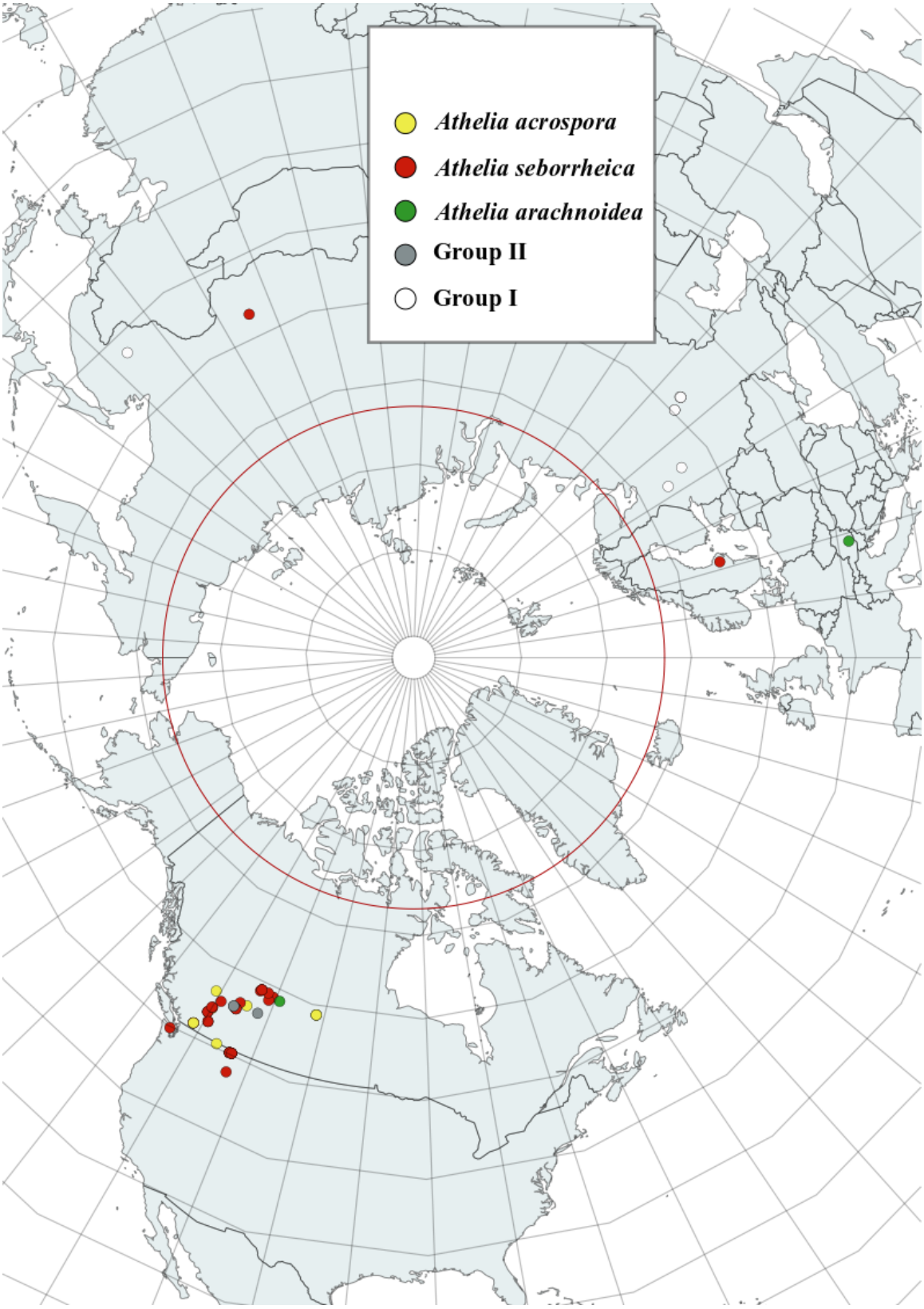


Figure 1 Map of *Athelia* collected and sequenced for this study, color-coded by species or group.

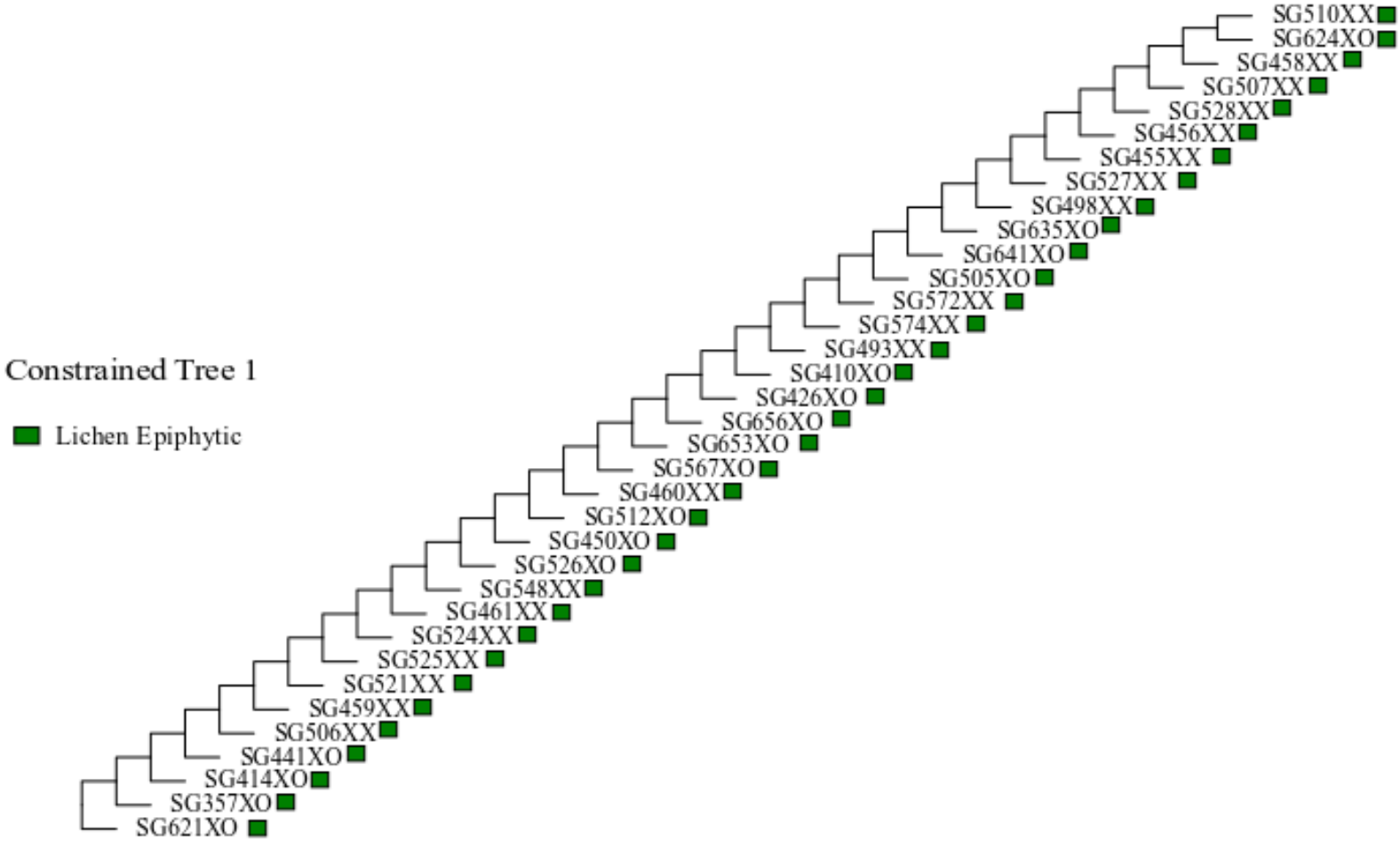


Figure 2 Constrained *Athelia* tree 1: *Athelia* from epiphytic lichen are monophyletic.

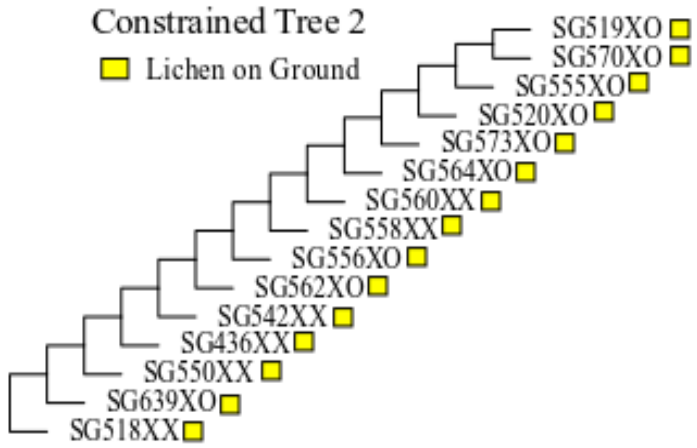


Figure 3 Constrained *Athelia* tree 2: *Athelia* from fallen lichen are monophyletic.

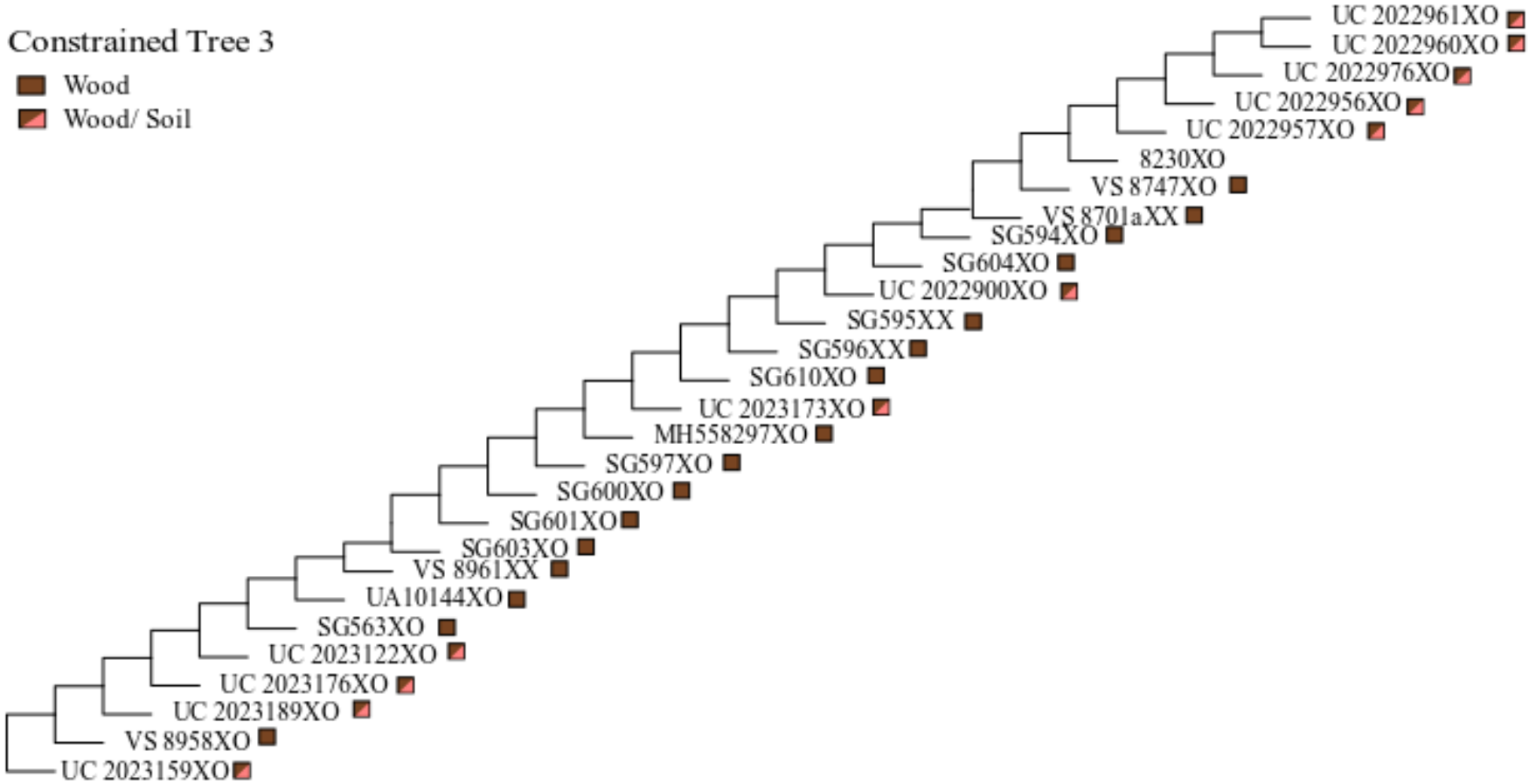
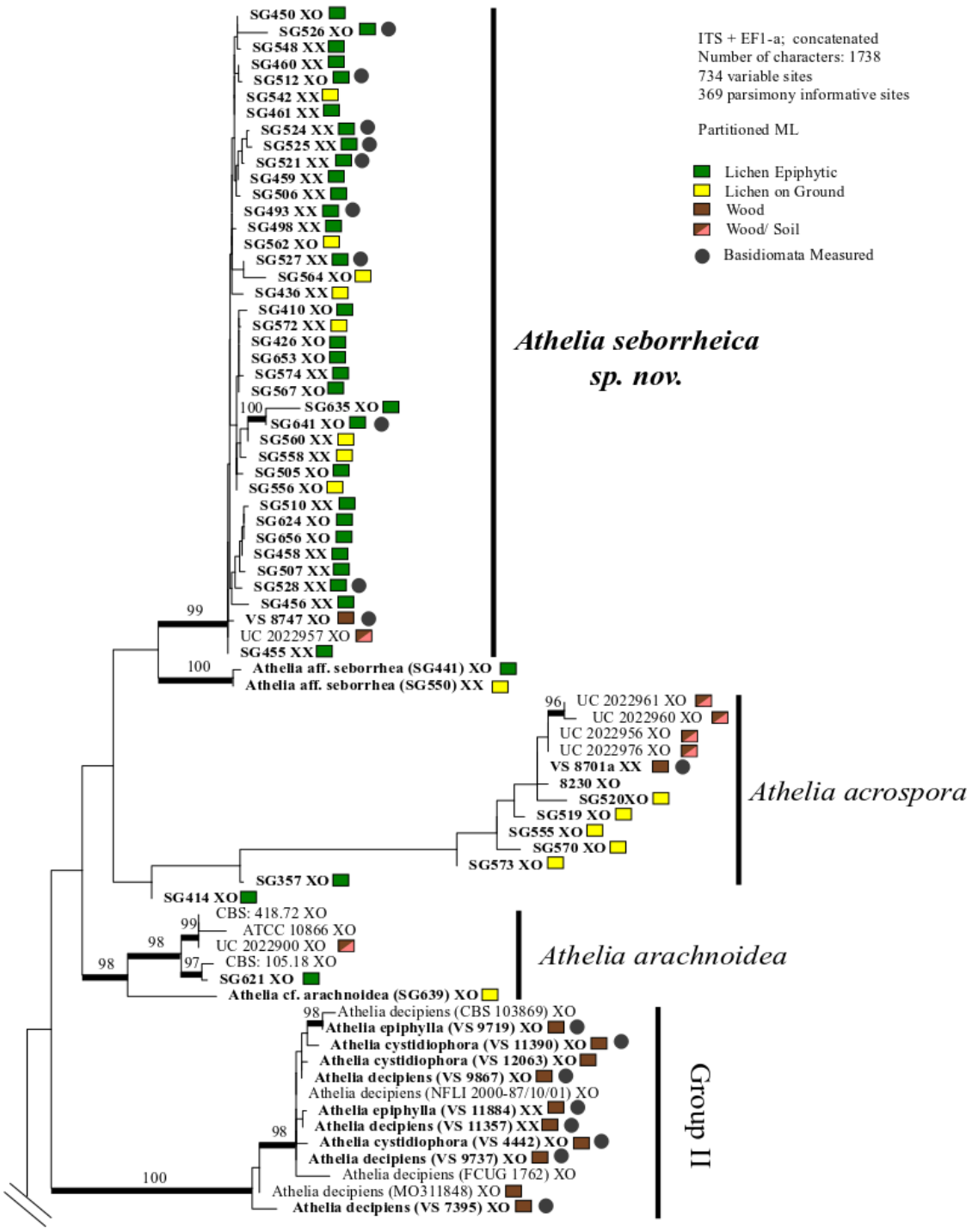


Figure 4 Constrained *Athelia* tree 3: *Athelia* from wood and soil are monophyletic.


ITS + EF1-a; concatenated
Number of characters: 1738
734 variable sites
369 parsimony informative sites
Partitioned ML
Lichen Epiphytic
Lichen on Ground
Wood
Wood/ Soil
Basidiomata Measured
Athelia seborrheica sp. nov.
Athelia acrospora
Athelia arachnoidea
Group II
SG450 XO
SG526 XO
SG548 XX
SG460 XX
SG512 XO
SG542 XX
SG461 XX
SG524 XX
SG525 XX
SG521 XX
SG459 XX
SG506 XX
SG493 XX
SG498 XX
SG562 XO
SG527 XX
SG504 XO
SG436 XX
SG410 XO
SG572 XX
SG426 XO
SG653 XO
SG574 XX
SG567 XO
SG635 XO
SG641 XO
SG560 XX
SG558 XX
SG505 XO
SG556 XO
SG510 XX
SG624 XO
SG656 XO
SG458 XX
SG507 XX
SG528 XX
SG456 XX
VS 8747 XO
UC 2022957 XO
SG455 XX
Athelia aff. seborrhea (SG441) XO
Athelia aff. seborrhea (SG550) XX
UC 2022961 XO
UC 2022960 XO
UC 2022956 XO
UC 2022976 XO
VS 8701a XX
8230 XO
SG520XO
SG519 XO
SG555 XO
SG570 XO
SG573 XO
SG357 XO
SG414 XO
CBS: 418.72 XO
ATCC 10866 XO
UC 2022900 XO
CBS: 105.18 XO
SG621 XO
Athelia cf. arachnoidea (SG639) XO
Athelia decipiens (CBS 103869) XO
Athelia epiphylla (VS 9719) XO
Athelia cystidiophora (VS 11390) XO
Athelia cystidiophora (VS 12063) XO
Athelia decipiens (VS 9867) XO
Athelia decipiens (NFLI 2000-87/10/01) XO
Athelia epiphylla (VS 11884) XX
Athelia decipiens (VS 11357) XX
Athelia cystidiophora (VS 4442) XO
Athelia decipiens (VS 9737) XO
Athelia decipiens (FCUG 1762) XO
Athelia decipiens (MO311848) XO
Athelia decipiens (VS 7395) XO
100
99
100
96
99
98
98
97
98
98
100

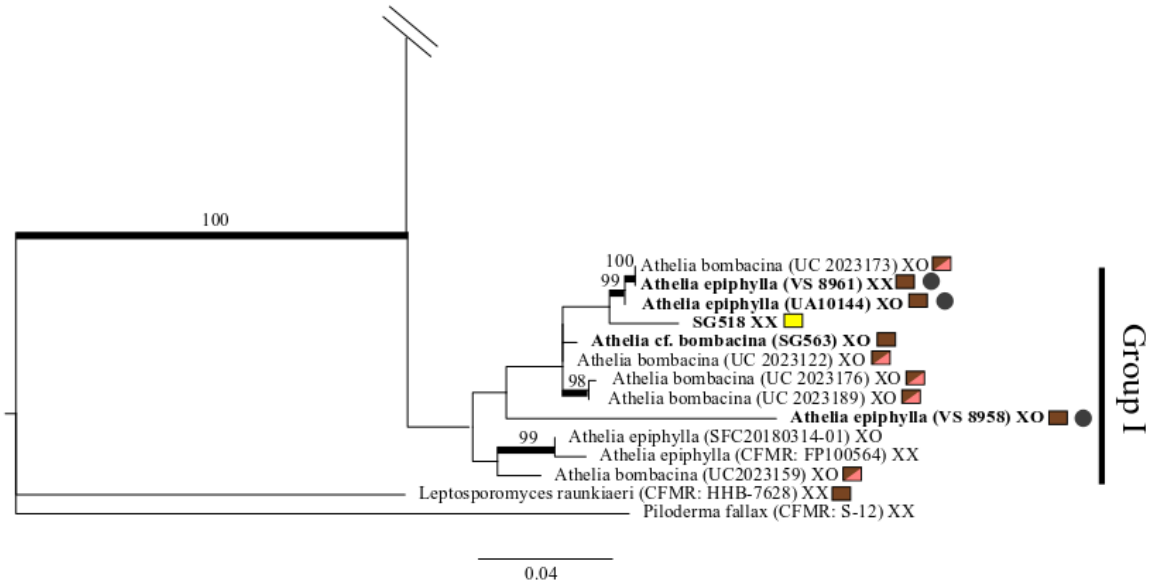
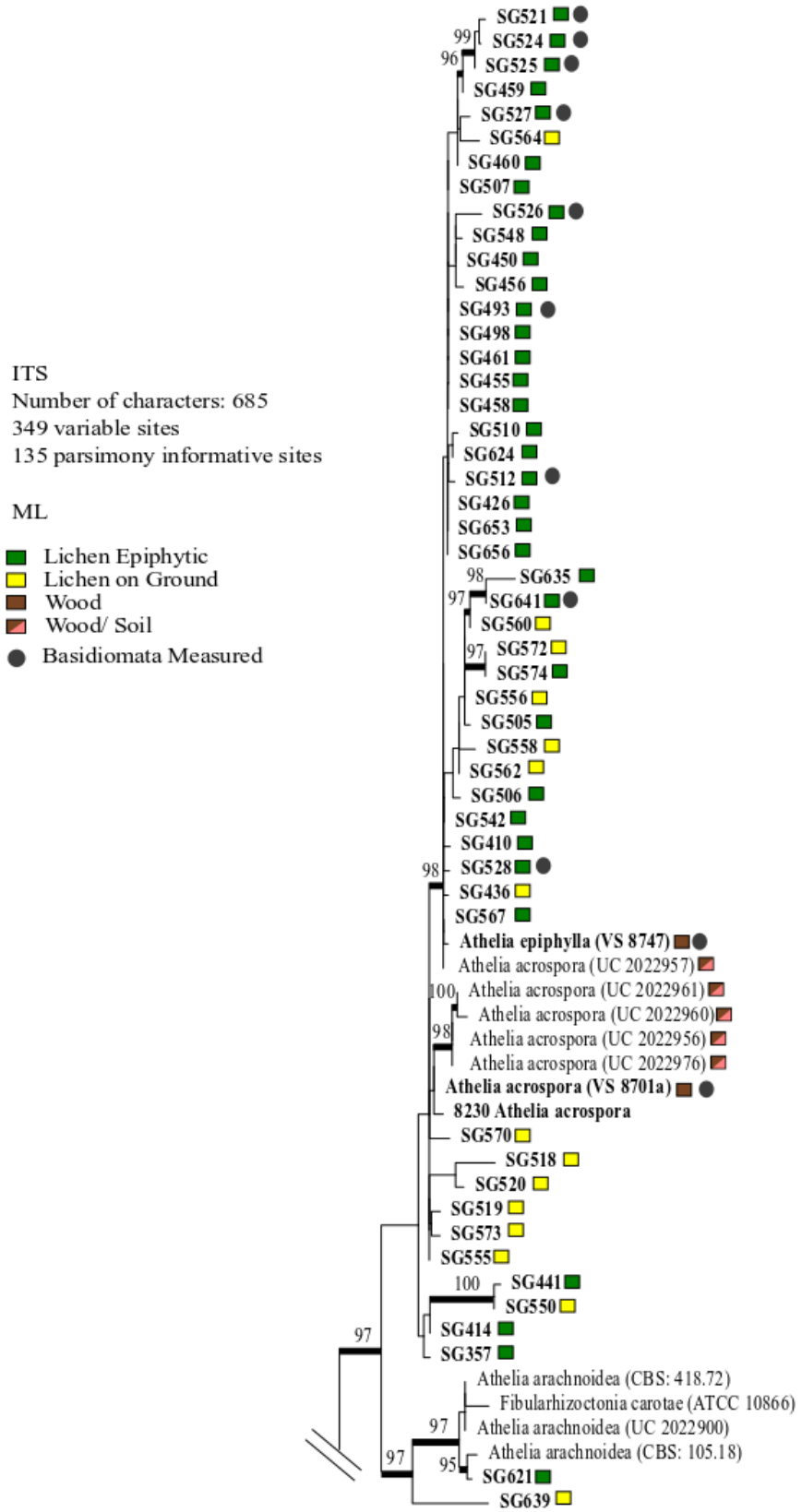


Figure 5 Concatenated ITS – EFI-α maximum likelihood (ML) *Athelia* tree. Branches with ultrafast bootstrapping support ≥95% indicated with bolded bars. Bolded tips indicate sequences and specimens new to this study. **X** = a given locus was successfully sequenced or available on GenBank for a given specimen; **O** = a given locus was not successfully sequenced or available on GenBank for a given specimen. **SG** refers to Spencer Goyette's DNA isolate numbers, **VS** refers to Viacheslav Spirin collection numbers.


ITS
Number of characters: 685
349 variable sites
135 parsimony informative sites
ML
Lichen Epiphytic
Lichen on Ground
Wood
Wood/ Soil
Basidiomata Measured
SG521
SG524
SG525
SG459
SG527
SG564
SG460
SG507
SG526
SG548
SG450
SG456
SG493
SG498
SG461
SG455
SG458
SG510
SG624
SG512
SG426
SG653
SG656
SG635
SG641
SG560
SG572
SG574
SG556
SG505
SG558
SG562
SG506
SG542
SG410
SG528
SG436
SG567
Athelia epiphylla (VS 8747)
Athelia acrospora (UC 2022957)
Athelia acrospora (UC 2022961)
Athelia acrospora (UC 2022960)
Athelia acrospora (UC 2022956)
Athelia acrospora (UC 2022976)
Athelia acrospora (VS 8701a)
8230 Athelia acrospora
SG570
SG518
SG520
SG519
SG573
SG555
SG441
SG550
SG414
SG357
Athelia arachnoidea (CBS: 418.72)
Fibularhizoctonia carotae (ATCC 10866)
Athelia arachnoidea (UC 2022900)
Athelia arachnoidea (CBS: 105.18)
SG621
SG639
99
96
98
97
97
98
100
98
100
97
97
97
95

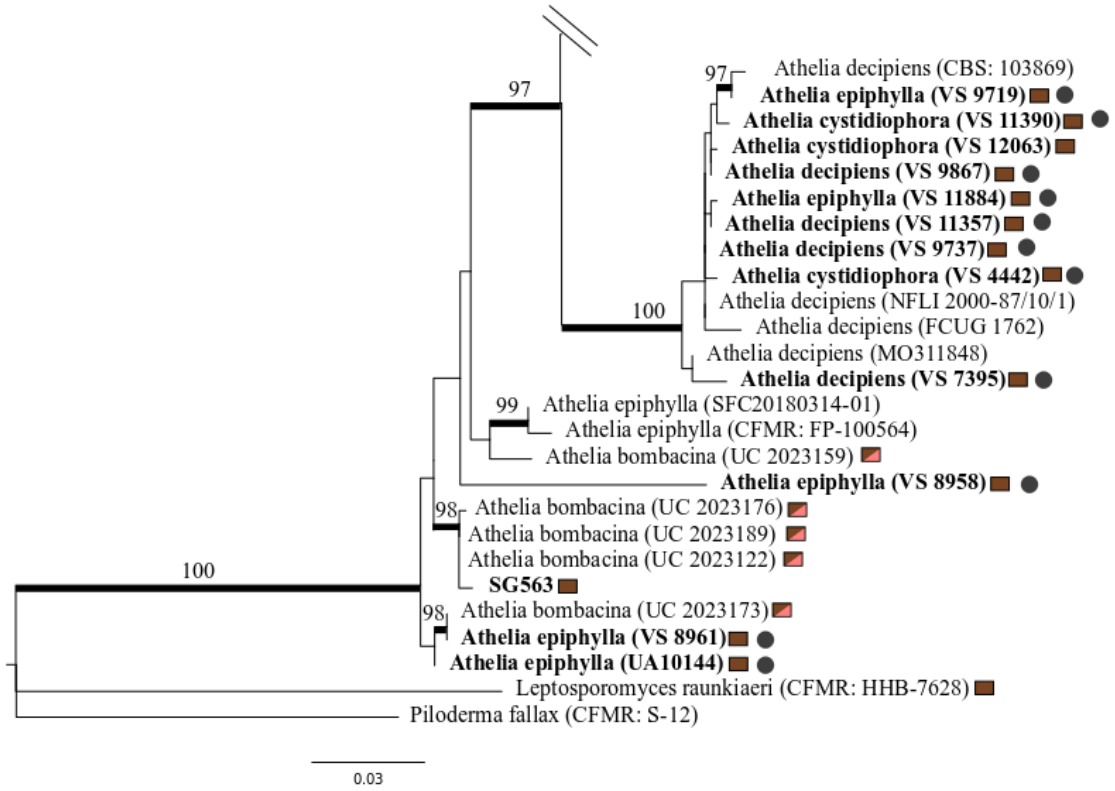


Figure 6 ITS maximum likelihood *Athelia* tree. Branches with ultrafast bootstrapping support ≥95% indicated with bolded bars. Bolded tips indicate sequences and specimens new to this study. **SG** refers to Spencer Goyette's isolate numbers, **VS** refers to Viacheslav Spirin's collection numbers.

Figure 7 EFI- α maximum likelihood *Athelia* tree. Branches with ultrafast bootstrapping support ≥ 95% indicated with bolded bars. Bolded tip branches indicate sequences and specimens new to this study. **SG** refers to Spencer Goyette's isolate numbers, **VS** refers to Viacheslav Spirin collection numbers.

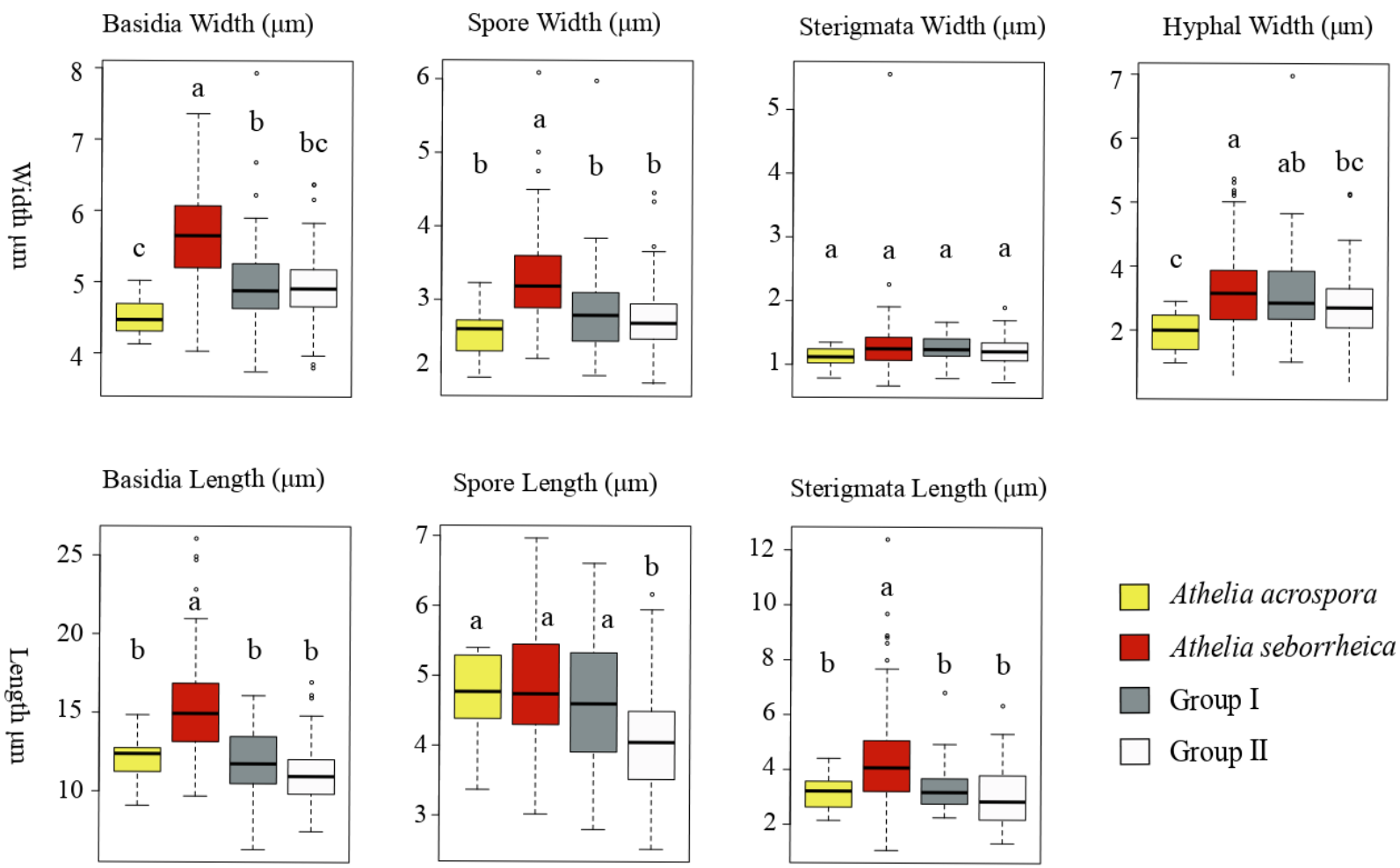
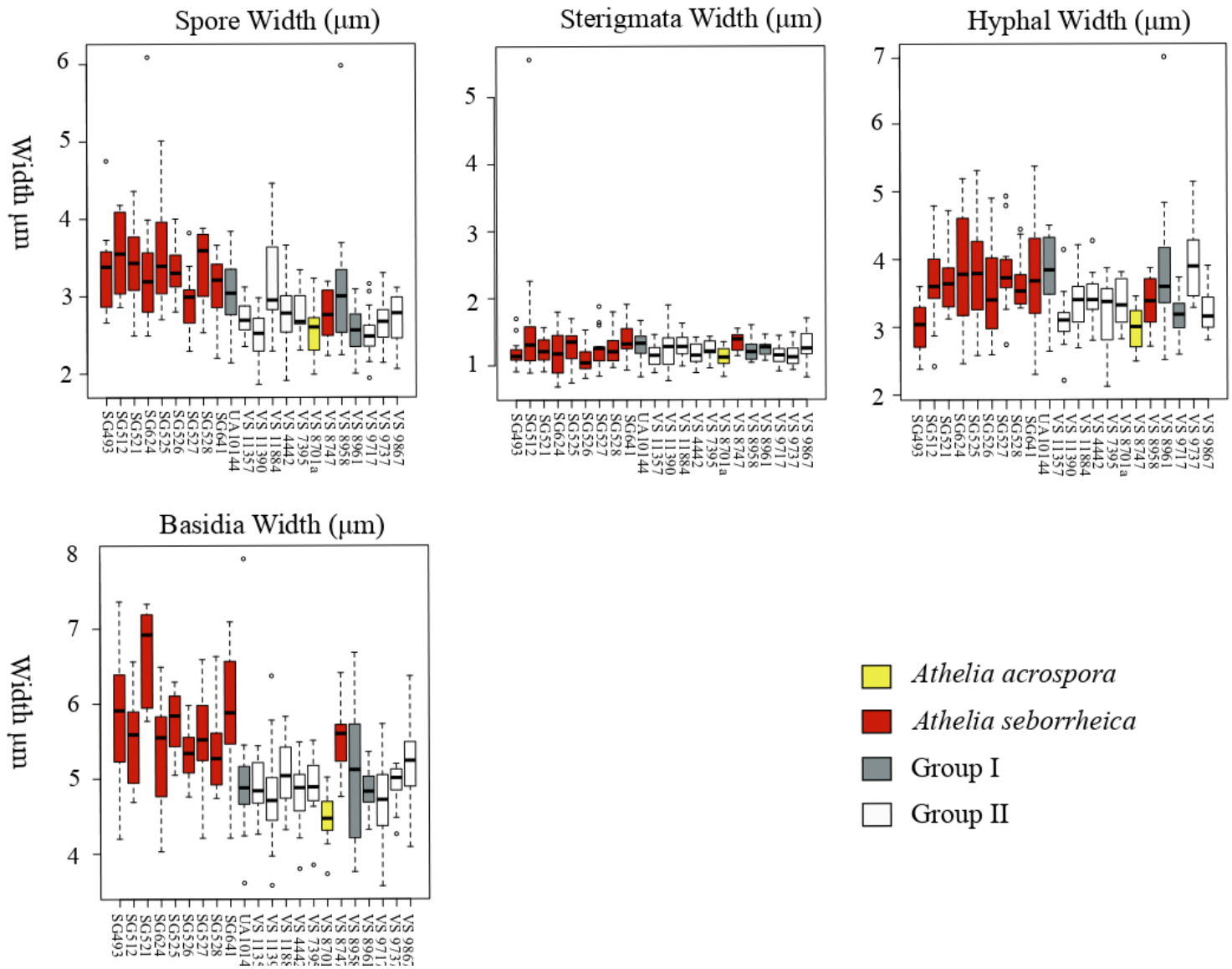

Basidia Width (µm)
Spore Width (µm)
Sterigmata Width (µm)
Hyphal Width (µm)
Width µm
Basidia Length (µm)
Spore Length (µm)
Sterigmata Length (µm)
Length µm
Athelia acrospora
Athelia seborrheica
Group I
Group II

Figure 8 Box and whisker plot of each measurement by clade. Tukey HSD differences indicated by letters above. Basidium width, basidium length, basidiospore width, and sterigmata length were significantly different between *A. seborrheica* and all other species or groups. Basidiospore length was significantly different between Group II and all other species or groups.


Spore Width (µm)
Sterigmata Width (µm)
Hyphal Width (µm)
Basidia Width (µm)
Width µm
SG493
SG512
SG521
SG624
SG525
SG526
SG527
SG528
SG641
UA10144
VS 11357
VS 11390
VS 11884
VS 4442
VS 7395
VS 8701a
VS 8747
VS 8958
VS 8961
VS 9717
VS 9737
VS 9867
Athelia acrospora
Athelia seborrheica
Group I
Group II

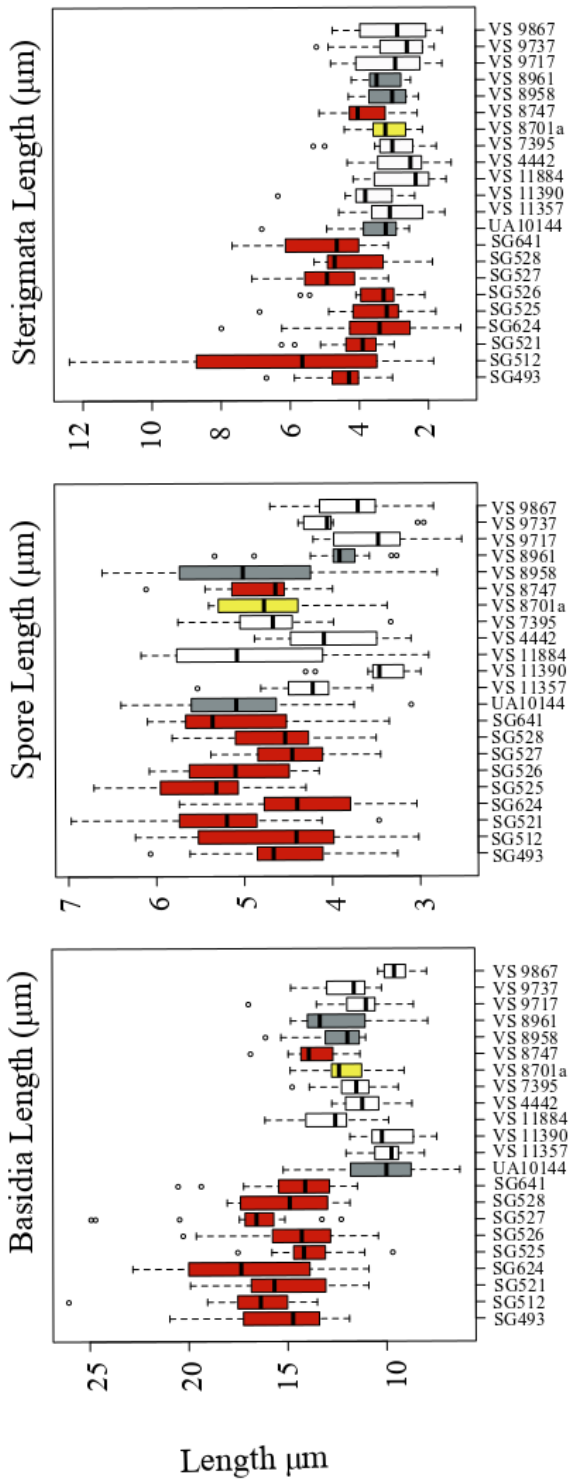


Figure 9 Box and whisker plot of all specimen measurements for a given morphological feature.

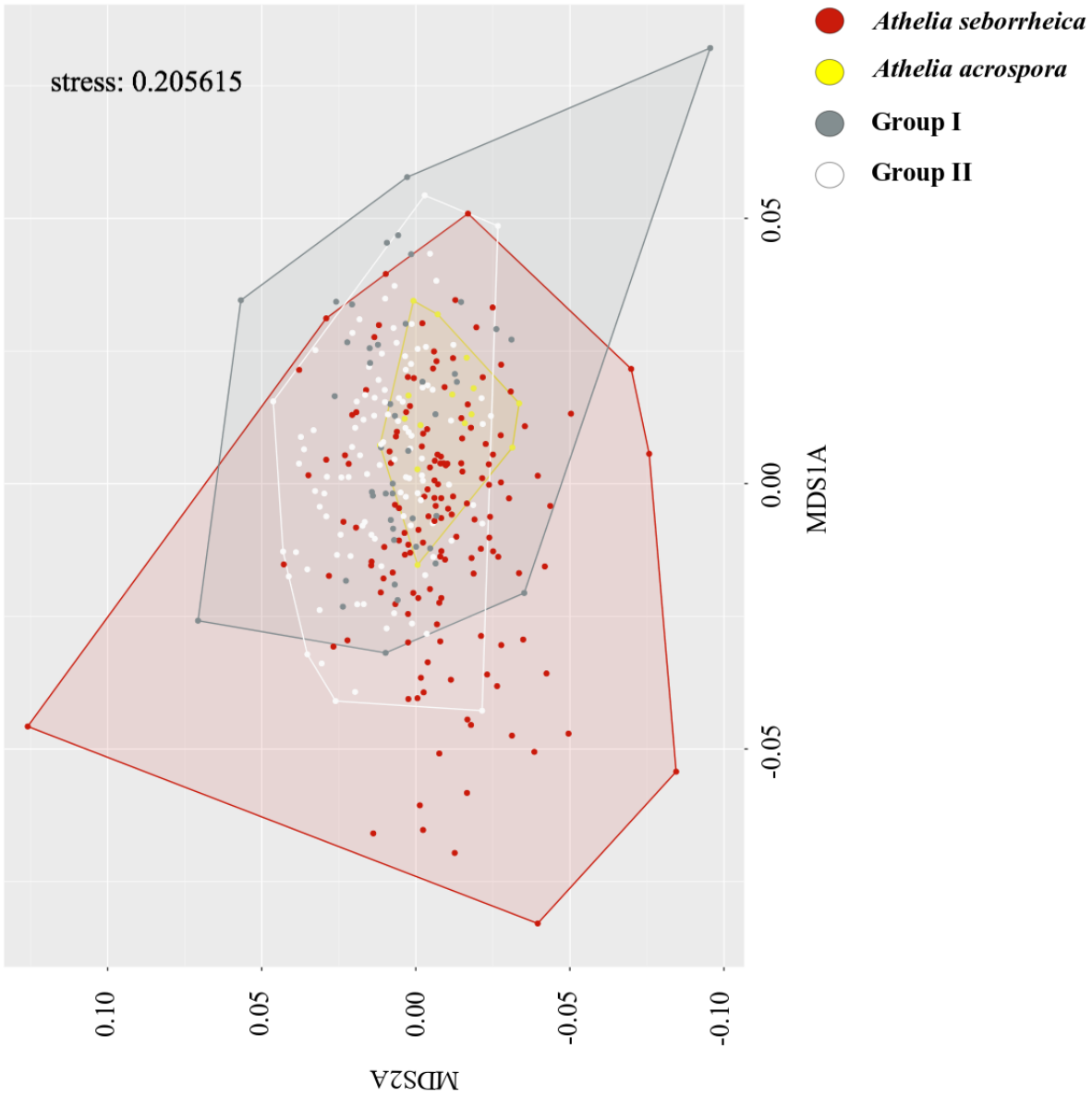
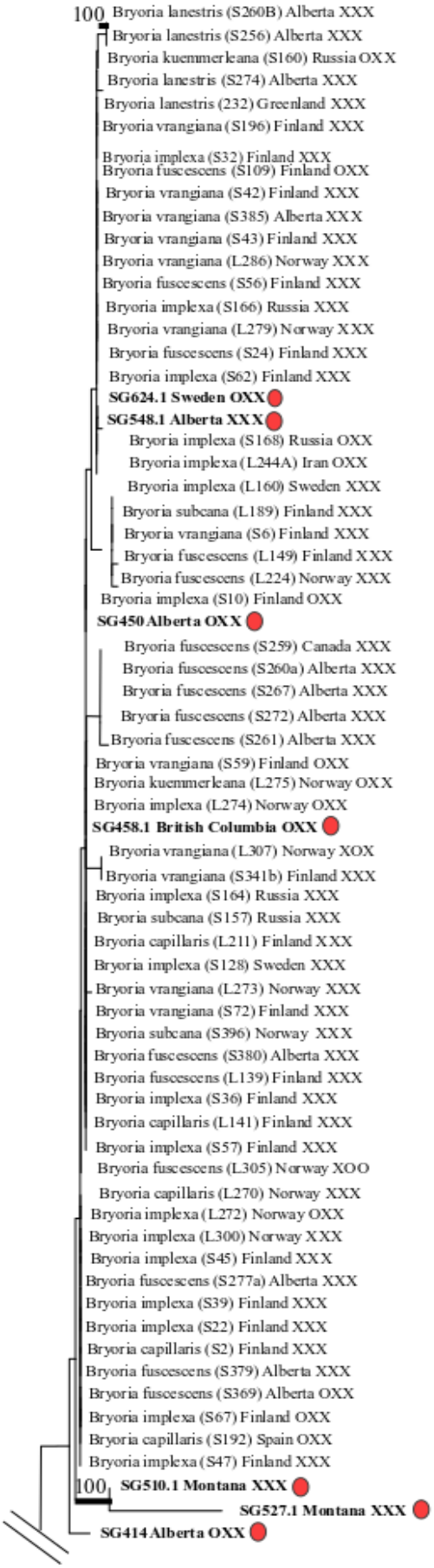


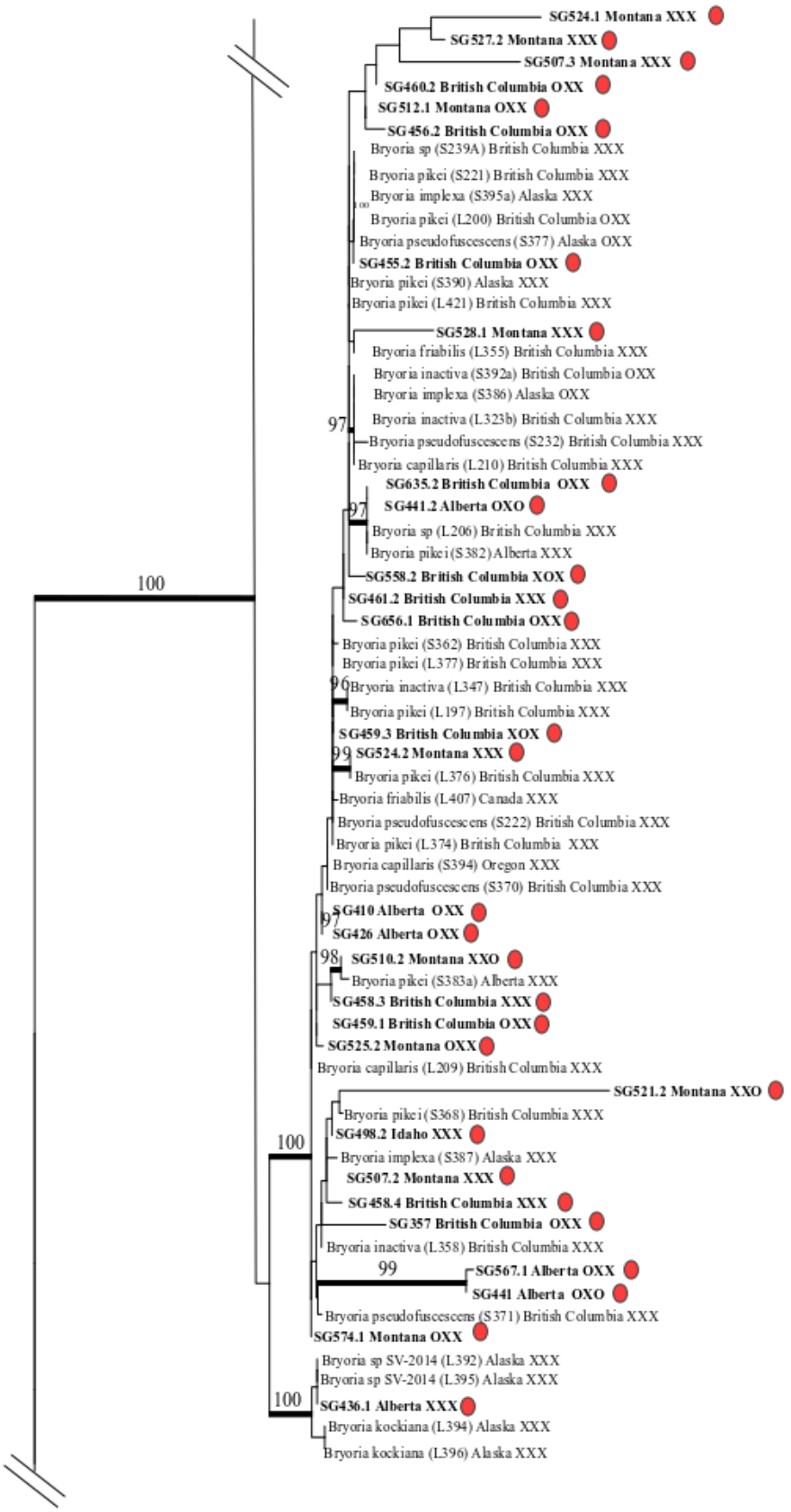
Figure 10 NMDS of *Athelia* morphological measurements calculated using "Euclidean" distances in two dimensions in the R package *vegan* (Oksanen et al., 2019). Hulls covering data points cover all points of a given species or grouping determined *a posteriori* to the generation of the concatenated tree in Fig. 2

ITS+ IGS + GAPDH, concatenated
Number of characters: 2018
469 variable sites
118 parsimony informative sites

Partitioned ML

● *Athelia* infected




SG524.1 Montana XXX
SG527.2 Montana XXX
SG507.3 Montana XXX
SG460.2 British Columbia OXX
SG512.1 Montana OXX
SG456.2 British Columbia OXX
Bryoria sp (S239A) British Columbia XXX
Bryoria pikei (S221) British Columbia XXX
Bryoria implexa (S395a) Alaska XXX
100
Bryoria pikei (L200) British Columbia OXX
Bryoria pseudofuscescens (S377) Alaska OXX
SG455.2 British Columbia OXX
Bryoria pikei (S390) Alaska XXX
Bryoria pikei (L421) British Columbia XXX
SG528.1 Montana XXX
Bryoria friabilis (L355) British Columbia XXX
Bryoria inactiva (S392a) British Columbia OXX
Bryoria implexa (S386) Alaska OXX
97
Bryoria inactiva (L323b) British Columbia XXX
Bryoria pseudofuscescens (S232) British Columbia XXX
Bryoria capillaris (L210) British Columbia XXX
SG635.2 British Columbia OXX
97
SG441.2 Alberta OXO
Bryoria sp (L206) British Columbia XXX
Bryoria pikei (S382) Alberta XXX
100
SG558.2 British Columbia XOX
SG461.2 British Columbia XXX
SG656.1 British Columbia OXX
Bryoria pikei (S362) British Columbia XXX
Bryoria pikei (L377) British Columbia XXX
96
Bryoria inactiva (L347) British Columbia XXX
Bryoria pikei (L197) British Columbia XXX
SG459.3 British Columbia XOX
99
SG524.2 Montana XXX
Bryoria pikei (L376) British Columbia XXX
Bryoria friabilis (L407) Canada XXX
Bryoria pseudofuscescens (S222) British Columbia XXX
Bryoria pikei (L374) British Columbia XXX
Bryoria capillaris (S394) Oregon XXX
Bryoria pseudofuscescens (S370) British Columbia XXX
97
SG410 Alberta OXX
SG426 Alberta OXX
98
SG510.2 Montana XXO
Bryoria pikei (S383a) Alberta XXX
SG458.3 British Columbia XXX
SG459.1 British Columbia OXX
SG525.2 Montana OXX
Bryoria capillaris (L209) British Columbia XXX
SG521.2 Montana XXO
Bryoria pikei (S368) British Columbia XXX
SG498.2 Idaho XXX
100
Bryoria implexa (S387) Alaska XXX
SG507.2 Montana XXX
SG458.4 British Columbia XXX
SG357 British Columbia OXX
Bryoria inactiva (L358) British Columbia XXX
99
SG567.1 Alberta OXX
SG441 Alberta OXO
Bryoria pseudofuscescens (S371) British Columbia XXX
SG574.1 Montana OXX
Bryoria sp SV-2014 (L392) Alaska XXX
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Bryoria kockiana (L396) Alaska XXX

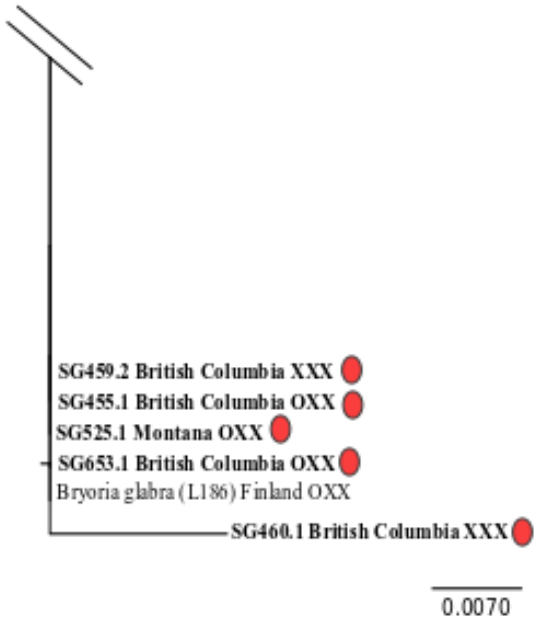

Figure 11 Concatenated ITS – IGS – GAPDH maximum likelihood Bryoria sect. Implexae tree. Branches with ultrafast bootstrapping support ≥95% indicated with bolded bars. Bolded tip indicate sequences and specimens new to this study. X = a given locus was successfully sequenced or available on GenBank for a given specimen; O = a given locus was not successfully sequenced or available on GenBank for a given specimen. SG refers to Spencer Goyette's isolate numbers.

Plate 1 Healthy *Bryoria sp.* Photo by Spencer Goyette.

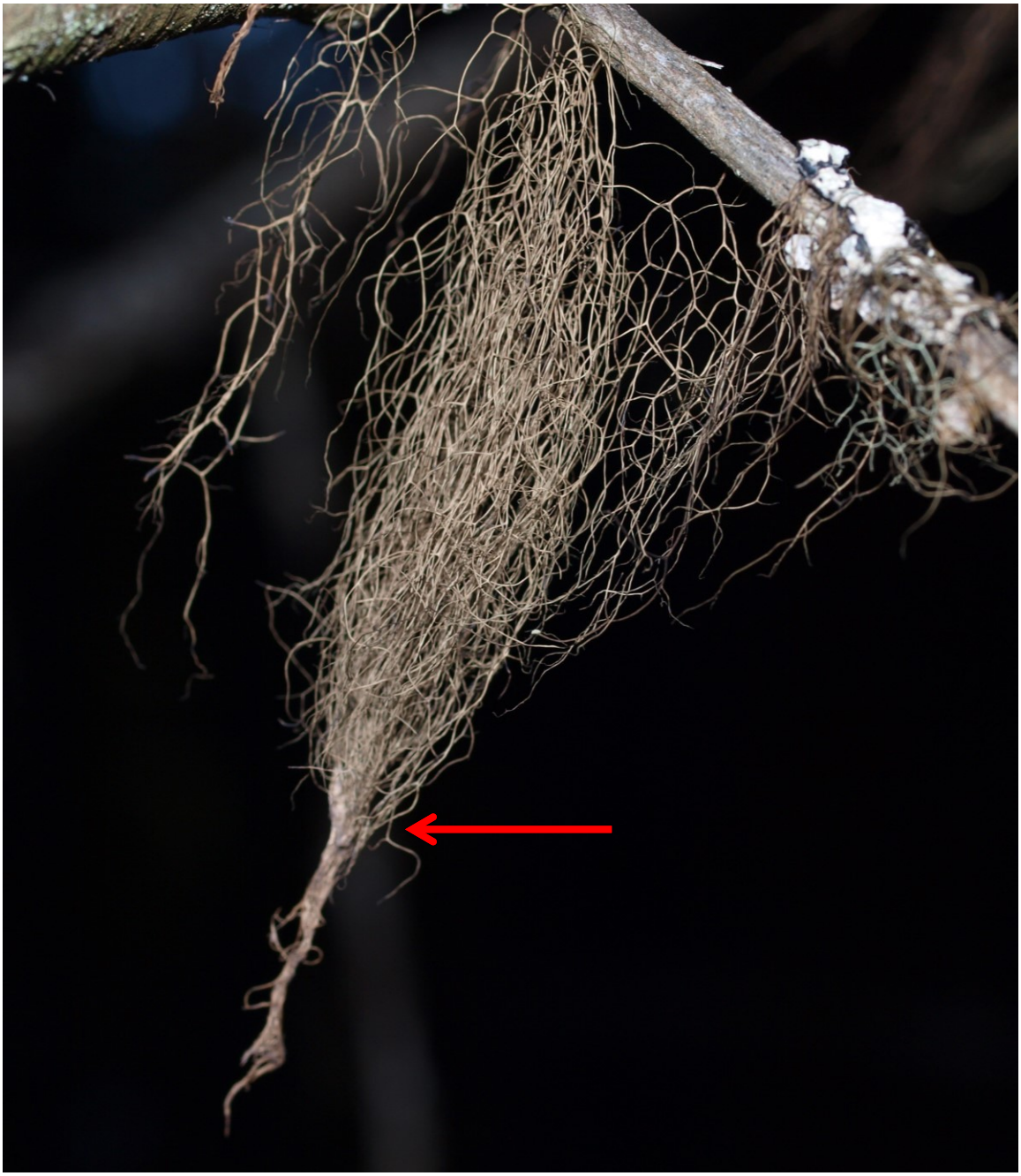

Plate 2 *Bryoria sp.* with rattail, indicated here with a red arrow. Photo by Spencer Goyette.

Plate 3 *Bryoria sp.* infected with an unknown fungal pathogen indicated here with red arrows. Note how the pattern of infection tracks the formation of rattails. Photo by Spencer Goyette.

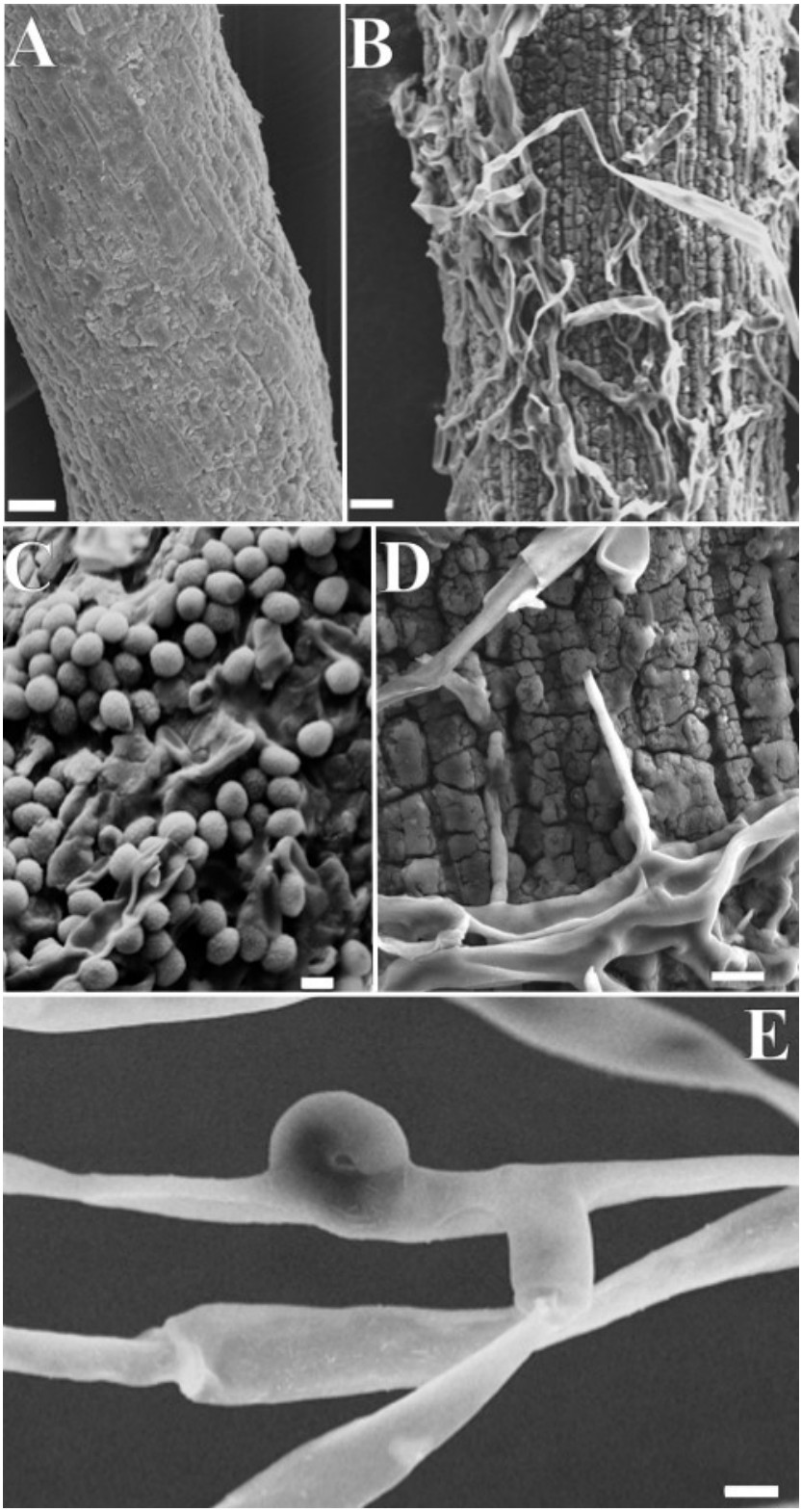

Plate 4 SEM micrographs taken on a Zeiss Sigma 300 VP-FESEM in the Department of Earth and Atmospheric Sciences at the University of Alberta.

A – Uninfected *Bryoria* thallus (scale bar 10 µm); **B** – *Bryoria* thallus infected with *Athelia seborrheica* (scale bar 10 µm); **C** – *Athelia seborrheica* basidiospores and basidia on *Bryoria* thallus (scale bar 2µm); **D** – Close up of *Athelia seborrheica* on *Byoria* thallus (scale bar 2µm); **E** – *Athelia seborrheica* clamp connection (scale bar 2µm). Images by Spencer Goyette.

Plate 5 *Athelia* on lichen from a fallen *Larix* branch, emerging just after snowmelt outside Trego, Montana. Photo by Toby Spribille.

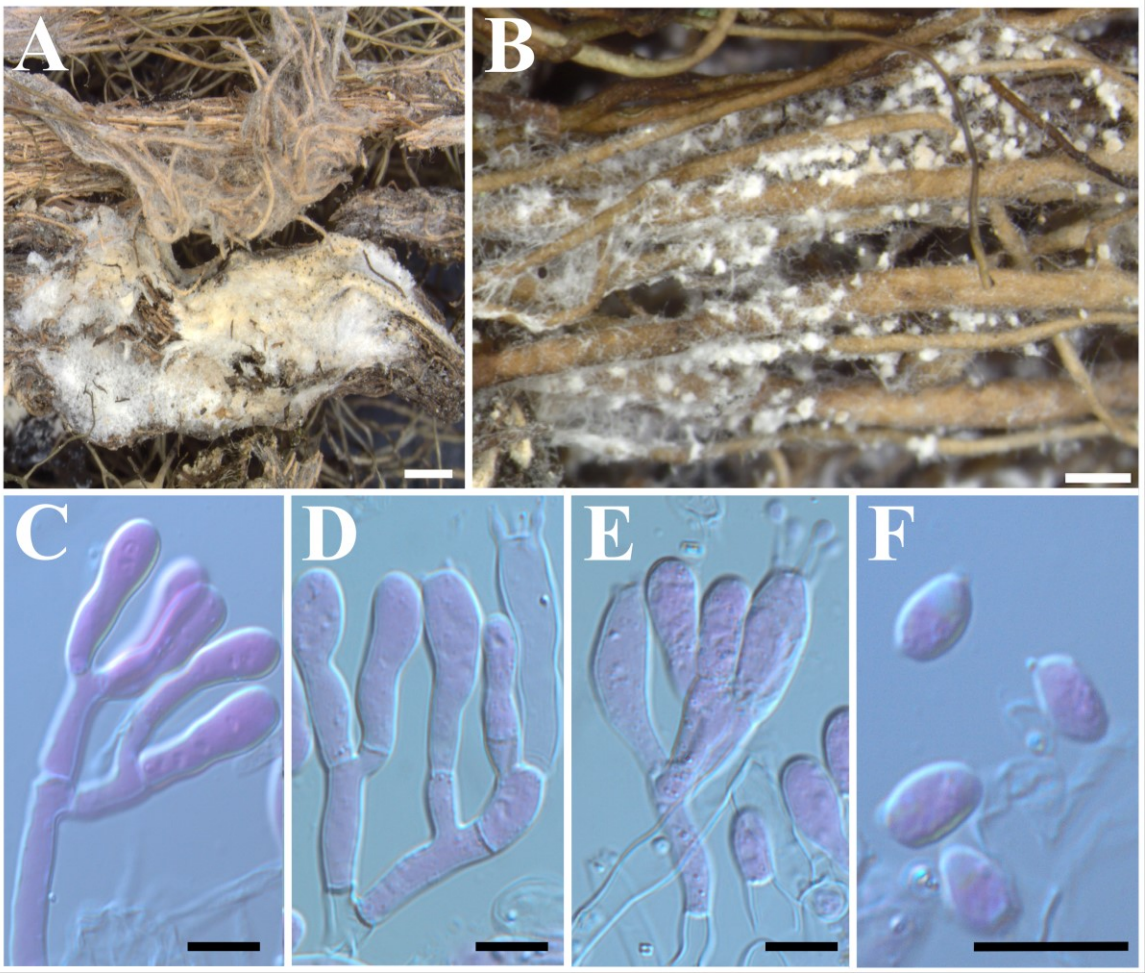

Plate 6 Basidiomata and sclerotia of *Athelia seborrheica*
A – basidioma on rattail (scale bar 1mm); **B** – sclerotia of *Athelia seborrheica* on rattailed *Bryoria* (scale bar 500µm); **C** – basidia (scale bar 10 µm); **D** – basidia with sterigmata (scale bar 10 µm); **E** – mature basidia with developing basidiospores attached to tips of sterigmata (10 µm); **F** – basidiospores (scale bar 10 µm). All squashes stained with 1% Phloxine-B in 5% potassium hydroxide.

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