

A MORPHOLOGICAL AND MOLECULAR REASSESSMENT
OF *ROBERGEA ALBICEDRAE* (ASCOMYCOTA)

by

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ABSTRACT

Historically, ascomycete fungi have been classified based on key morphological characteristics such as spore size and shape, ascus morphology, and biochemical indicators. This approach has resulted in groups of organisms that are microscopically and macroscopically similar, however, in some situations these groupings are not supported by the results of modern phylogenetic studies. *Robergea albicedrae* is a fungus that grows on the bark and twigs of a single species of tree, the Ashe juniper (*Juniperus ashei*). First described in 1910, the fungus has been reassigned at the generic and family levels several times over the past century and is now classified in Stictidaceae. The goal of this study was to provide new morphological and molecular data to better understand the life cycle and relationships of the species. Procedures were designed to culture the fungus both *in situ* and *in vitro*. Plastic coverslips were placed on the bark of Ashe juniper for 17 months in an attempt to document the stages of the life cycle of the fungus. Samples of *Robergea albicedrae* were also cultured using a variety of media and plating techniques. *Robergea albicedrae*, along with a diversity of other fungi, was successfully grown on coverslips and in pure culture. *Robergea albicedrae* was also sequenced and analyzed at the 18S SSU rDNA and ITS 1 and 2 regions. Analyses of these sequences using Bayesian phylogenetics provided strong support for the placement of *Robergea albicedrae* in the order Ostropales and the family Stictidaceae of the class Lecanoromycetes.

I. INTRODUCTION

There are currently approximately 120,000 fungal species known to science, however it is estimated that there may actually be as many as 3.8 million species (Hawksworth and Lücking 2017). Fungal systematics is a dynamic field, and traditional placements of fungal species based on uninformative characters must be revised to incorporate evolutionarily informative characters. The identification of fungi has historically been based on morphology, specifically for ascomycetes, on the ascus and spores. For fungal endophytes and epiphytes, identifications and understanding of systematic relationships are most reliable when molecular and morphological data are combined (Ko et al. 2011; Lumbsch and Leavitt 2011).

This study is focused on a relatively little studied fungus, *Robergea albicedrae* (Ascomycota). The current taxonomic placement of this species in the family Stictidaceae (Ostropales) is based on the following morphological characters: perithecia 1.5 x 0.5 mm, gray when young then maturing to carbonaceous black, immersed in stromatic nodules of host tissue present on the bark and decorticated wood, arranged parallel to host surface with a definitive ostiole present and curving outward, the forcibly discharged spores eight in number, filiform and multiseptate, approximately 800 x 2 µm (Sherwood 1977).

Initially described in 1910 as a new fungal endophyte, *Cyanospora albicedrae* was thought to possibly be a parasite on Ashe junipers (*Juniperus ashei*), although there was no concrete evidence it harms the trees (Heald and Wolf 1910). The species was reassigned by Saccardo and Traverso (1911) to the genus *Robergea* in the family Hysteriaceae, although Plunkett et al. (1923) maintained the species in *Cyanospora* but

placed it in the family Ceratostomataceae.

The host organism for *R. albicedrae* is the Ashe juniper, which can be found growing throughout central Texas with a range that extends south into northern Mexico and north through Texas, southern Oklahoma, and into northern Arkansas (Figure 1). Ashe juniper is a hardy, tolerant species that grows primarily on rocky, shallow soils derived from limestone or granite (Vines 1960). Ashe junipers play a complicated and important role ecologically, the mature trees providing important nesting materials for endangered golden-cheeked warblers and a food source for wildlife (Kroll 1980). Economically, Ashe junipers can have considerable impact. As these plants encroach on native grass and rangelands, species diversity can decrease and result in a considerable investment in terms of time and money to remove them (Yager and Smeins 1999).

Robergea albicedrae appears to be host-specific and has not been found to grow independently or in association with any organism other than *Juniperus ashei*. White patches of fungus that grow on the bark of *J. ashei* are a common diagnostic character for this tree and can be used to distinguish Ashe junipers from other juniper species that grow in the area, such as *J. virginiana*. The fungus has been found growing on the bark of both twigs and the trunk of the trees. Young twigs are often completely encircled by the fungus with damage occurring to the cambium layer of the twig (Heald and Wolf 1910, 1912). Most casual observers have concluded that the fungus may be parasitic, although studies of others in Stictidaceae have shown a dynamic relationship in terms of nutrient assimilation, for example, the colonization of existing dead twigs as saprotrophs, “optional lichenization,” and parasitic endophytism (Wedin et al. 2004; Baloch et al. 2010; Muggia et al. 2011).

The genus *Robergea* contains ten species and, based on morphology, species in this genus are very similar to members of the genera *Stictis* and *Ostropa* (Sherwood 1977). All the species of *Robergea* are rare and inconspicuous except for *Robergea albicedrae*, which is very common in Texas and Mexico. Some of the key characteristics of *R. albicedrae* are the embedded perithecium with a small offset ostiole for spore dispersal and the unique length and shape of the spores (Sherwood 1977). Virtually no microscopy work has been done to determine the nature of the hyphal growth. Microscopy (light and confocal) of *R. albicedrae* was done to get good quality images to supplement the line drawings currently available in the literature.

Sequence data is very limited for this genus and no sequence data was available for *R. albicedrae* in GenBank (Clark et al. 2016). Only one other taxon in *Robergea* was available in GenBank, *R. cubicularis*, and its sequence data was incomplete. Several advances in fungal molecular research have come about in the last 20 years, one of the most meaningful being the assignment of internal transcribed spacers (ITS) as the universal barcode locus for describing relationships between species (Mitchell et al. 1995; Hibbett and Taylor 2013). Using the most common and successful primers for Ostropalean fungi, sequence data was collected for *R. albicedrae* and submitted to NCBI for future use by other researchers. Most fungal tree of life projects need an increase in the depth and breadth of sequence data available. By adding this data, information about this genus and family will help support fungal and plant diversity research. In addition to the sequence data for *R. albicedrae*, recording the diversity of endophytic fungi and bark inhabiting algae will help to broaden our perspective on microhabitats and deepen our understanding into the complex relationship organisms have with each other.

Current research in the family Stictidaceae, along with the widespread occurrence of the fungus in central Texas, prompted the following goals: 1) to obtain new morphological information to clarify currently unsupported claims in terms of nutrient assimilation (saprotroph or parasite); 2) to better understand the taxonomic placement of *Robergea albicedrae*, currently based on morphological characteristics, with molecular data; and 3) to build a phylogeny based on molecular data for *R. albicedrae*.

II. MATERIALS AND METHODS

Field Collection

Samples for morphological and anatomical study were collected from Spring Lake Natural Area, in San Marcos, Texas, at monthly intervals from September 2017 to February 2018. Bark and twig samples were removed from trees showing a high density of fungal growth. Bark was removed and stored in paper bags. Young, decorticated twigs were cut and stored paper bags. Samples were taken from random visual selections of at least 15 trees during each collection event. Samples were promptly relocated to the lab and stored in glass jars and vials containing FAA (90:5:5 50% EtOH: glacial acetic acid: formalin 10%).

Samples for DNA extraction were collected fresh, in December 2017 from multiple trees from Spring Lake Natural Area. Ascocarps were excised using a sterile blade using aseptic technique and stored in sterile microcentrifuge tubes at -80°C until extraction. In spring 2019, bark and twig samples were collected within the range of Ashe juniper; the collection data is presented in Table 1 and the collection localities are mapped in Figure 2.

Table 1. *Robergea albicedrae* collections for DNA analysis. Samples jrb001-jrb011 include one collection event with a small number of ascocarps collected due to low fruiting bodies on the bark. Samples jrb004a/b and jrb012-016a/b had two samples collected from each individual tree. These trees had a high number of fungal ascocarps present on the bark.

Sample	Date	Location	GPS Coordinates
jrb_001	12/19/2018	OK: Murray Co.	N 34.4216° W 97.1336°
jrb_002	12/19/2018	OK: Murray Co.	N 34.4031° W 97.1421°
jrb_003	12/17/2018	TX: Sutton Co.	N 30.614940° W
jrb_004A/B	01/14/2019	TX: Blanco Co.	100 7151200 N 30.2055° W 98.3766°
jrb_005	01/14/2019	TX: Lampasas Co.	N 31.0927° W 98.1898°
jrb_006	01/14/2019	TX: McCulloch Co.	N 31.4339° W 99.1698°
jrb_007	01/14/2019	TX: McCulloch Co.	N31.0146° W 99.2762°
jrb_008	01/14/2019	TX: Gillespie Co.	N 30.4429° W98.9766°
jrb_009	02/06/2019	TX: Comal Co.	N 29.7970° W 98.3324°
jrb_010	02/06/2019	TX: Kendall Co.	N 29.8128° W 98.7142°
jrb_011	02/06/2019	TX: Hays Co.	N 29.903854° W
jrb_012A/B	06/03/2019	TX: Hays Co.	00 0027570 N 29.9034° W 97.9298°
jrb_013A/B	06/03/2019	TX: Hays Co.	N 29.9028° W 97.9294°
jrb_014A/B	06/03/2019	TX: Hays Co.	N 29.9026° W 97.9297°
jrb_015A/B	06/03/2019	TX: Hays Co.	N 29.9023° W 97.9297°
jrb_016A/B	06/03/2019	TX: Hays Co.	N 29.9022° W 97.9298°

***In Situ* Coverslip Observations**

Two sets of *in situ* growth observations were established at a private residence outside San Marcos. Plastic coverslips, 22 mm² square, were placed on the bark of mature *Juniperus ashei* trees to observe colonization by and the growth cycle of *Robergea albicedrae*. Two sets of observations were conducted following methods in Sanders (2005) with some modifications. The first set of coverslips was placed in the field on 15 Dec 2017 and secured to the tree trunks using burlap strips cut to the length of the circumference of the tree and fastened using staples. The coverslips were slid behind the burlap, between the tree and cloth. For each of six mature trees, 15 coverslips were positioned between the bark and burlap. On 15 Mar 2018, 15 Jun 2018, 12 Oct 2018, and 06 Feb 2019, three coverslips from each tree were carefully removed (to prevent scratching the surface and removing any growth structures) from the burlap and brought back to the lab for observation. Each coverslip was prepared as a wet mount and viewed with a Nikon SMZ1000 dissecting scope and Nikon Eclipse 50i light microscope. Digital photographs taken with a Nikon Digital Sight DS-Fi1 camera system. Burlap and staples were removed after the collection of the last sample.

The second set of observations was established on 04 Jan 2018. Fiberglass mesh screens measuring 25 x 7 cm were used to mount coverslips and then fastened to the trunks of *J. ashei* trees using cotton ties. Mesh screens were placed on the same trees that had burlap/coverslip bands. Diagonal slits (9mm) were cut in the screen to allow the corners of the coverslips to be tucked in. Each mesh panel held 18 coverslips. On 08 Apr 2018, 08 Jun 2018, 12 Oct 2018, and 06 Feb 2019, three coverslips were removed, viewed, and photographed. Cotton ties and mesh were removed after the last sample was

collected. Images from the slides were recorded with the equipment listed above.

Anatomical Observations

For general anatomical observations, FAA preserved material was dehydrated through a tert-butanol series, embedded in paraffin, and thin sectioned ($\sim 10\mu\text{m}$) on a AO Spencer Model 820 rotary microtome. Ribbons were mounted on slides using albumen adhesive and floated into place using 4% formalin. Samples were then deparaffinized and stained (Triarch quadruple stain: safranin, fast green, orange G, and crystal violet) following standard botanical techniques (Johansen 1940; Ruzin 1999).

Localization of the fungal mycelium within the wood of *Juniperus ashei* was attempted using three staining techniques: trypan blue, aniline blue, and wheat germ agglutinin (Bhadauria et al. 2010). Fresh twigs and branches with visible fungal perithecia were cut to size (approx. 25 mm) and thin sections cut on an AO Model 860 sliding microtome. Sections were cut to 25 μm thickness and stored temporarily in distilled water until staining (within the hour). Care was taken to get transverse and longitudinal sections of the fruiting bodies. In order to prevent tearing of the wood sections, a thin coat of a polystyrene solution was painted on the wood surface between each cutting pass. The solution was prepared daily by adding small pieces of expanded polystyrene to 1–2 ml of butyl acetate (Barbosa et al. 2010). The solution was stirred, and small pieces of expanded polystyrene were added until a saturated solution was obtained.

Trypan blue stain was made to a 0.05% w/v concentration using DI water. Wood sections were soaked in the dark overnight then de-stained in three washes of DI water, mounted in 30% glycerol, and the coverslips were sealed with clear nail varnish. Aniline blue stain was made to a 0.05% w/v concentration in 150 mM KH_2PO_4 at pH 9.5. Samples were stained overnight, de-stained in three washes (15 minutes each) of 150 mM KH_2PO_4 , pH 9.5, and mounted as above. Combination samples were processed in trypan stain overnight, then soaked in aniline blue for four hours. Combination stain samples were then processed and mounted as above.

Wood sections stained with trypan blue and/or aniline blue were viewed using a Nikon Eclipse 50i light microscope and digital photographs taken with a Nikon Digital Sight DS-Fi1 camera system. Samples were also examined using an Olympus Fluoview FV1000 confocal laser scanning microscope (Olympus America, Center Valley, PA) with the UPLSAPO 10X NA:0.40 and 20X NA:0.75 objectives. Samples were scanned with a diode laser with an excitation line of 405 nm, emission wavelength of 461 nm, and intensity of 4.6%. Samples were also scanned with an argon laser with an excitation line of 488 nm, emission wavelength of 520 nm, and intensity of 10.9%. Scan speed was between 10 and 20 $\mu\text{s}/\text{pixel}$ and z-stack images were collected at 1.04 – 1.24 $\mu\text{m}/\text{slice}$. Images were processed using Fluoview FV1000, and the figures shown are z-stack images compressed into one image.

Samples to be stained with wheat germ agglutinin were thin sectioned at 25 μm on a sliding microtome and by hand using a dissecting scope. Half of the sections were fixed in FAA and the other half in 3% glutaraldehyde for 24 hours at room temperature. Samples were stained with wheat germ agglutinin (WGA), a fluorescent lectin stain that

binds to chitin (Kristiansen et al. 1999). A 10 mg/mL stock solution was prepared of fluorescein WGA (Vector Laboratories Burlingame, CA), with a maximum excitation of at 495–500 nm and maximum emission at 514–521 nm. The stock solution was prepared with phosphate-buffered saline (PBS, pH 7.5). Thin sections were removed from FAA, washed once in PBS, then stained in WGA for 15 minutes in the dark. Samples were then dehydrated in 75%, 90%, 100% ethanol (5 minutes each), washed in water 4X (10 minutes each), mounted in glycerol, and coverslips affixed with clear nail varnish.

WGA-stained thin sections were viewed using the confocal laser scanning microscope with 20X NA:0.75 objective. Samples were scanned with an argon laser with an excitation line of 515 nm, emission wavelength of 527 nm, and intensity of 10.5%. Scan speed was 8 μ s/pixel and z-stack images were collected at 1.12 μ m/slice.

Pruina Composition Test

A common morphological characteristic used in fungal and lichen systematics is the presence or absence of a pruina. Pruinose fungi are described as having a white or frosty layer on their surfaces (Hale and Cole 1988). Pruinae are made up of an epinecral layer of dead hyphal cells and calcium oxalate in two forms, weddellite and whewellite (Wadsten and Moberg 1985) and there are multiple hypotheses about the source and function of these surface calcium oxalate crystals (Heiðmarsson 1996). The aim of this test in relation to *R. albicedrae* is to determine the composition of the white, powdery material associated with this fungus and ascertain if it constitutes pruina, which could, in turn, be used as a taxonomic feature (Garty et al. 2002).

The standard of synthetic whewellite produces an absorption peak at wavenumber 1317 cm and that of weddellite at 1326 cm (Lewis et al. 1974). The white crystals could

also indicate the presence of gypsum, which would be identified by absorption peaks at 601 and 669 cm (Hunt et al. 1950). Other absorption peaks could be produced due to hyphal fragments, bark, dust, and other sources of contamination (Garty et al. 2002).

Three individual trees were sampled from Spring Lake Natural Area. Several samples of bark and twigs from *J. ashei* trees were collected and pooled into one sample for that individual tree. Surface powder from these samples was scraped to produce enough powder (approx. one gram) to analyze using a Fourier transform infrared spectrometer, Brunker Alpha II Platinum-ATR (Department of Chemistry and Biochemistry, Texas State University). The background spectrum was taken with air and the check signal measurements were; amplitude: -2295, position: 999844. The powdered sample was scraped and collected into the viewing window of the diamond ATR plate. The infrared spectra were recorded along with the location of the main peak maxima. The diamond ATR plate was carefully cleaned with isopropyl alcohol and a clean soft cloth between samples.

Isolation of Pure Fungal Cultures

An effort was made to obtain pure cultures of *R. albicedrae* using several different types of culture media, including a bark extract, malt extract agar (MEA), and MEA plus bark extract. The bark extract was prepared using 40 g of *J. ashei* bark and twigs cut into small pieces and added to 500 mL of DI H₂O and boiled for 60 minutes (Vobis 1977). This solution was then filtered and stored at 4°C. The extract was used to prepare the following media for the fungal isolation: MEA, MEA + bark extract, 100% bark extract, 50% bark extract, and 10% bark extract. All plates were made with a final antibiotic concentration of 20 µg/mL chloramphenicol.

Three methods were used to prepare fungal samples for isolation and each preparation was plated in triplicate on the five different types of media described above, resulting in a final plating of 45 samples. The first method entailed collecting approximately 20 ascocarps that were rinsed in DI for 24 hours, then ground in a sterilized mortar with sterile nuclease-free water. The resultant macerate was then streaked onto sterile plates. Additional samples were prepared by placing approximately 20 ascocarps on the inner surface of the lid of a sterile petri dish, which was then inverted to allow the spores to be discharged upwards onto the agar surface for 24 hours. The lids were then carefully removed and replaced with new lids. The final samples were prepared by using sterile instruments to dissect open an ascocarp, exposing the spores, then placing a small piece (approx. 1mm^3) of perithecial tissue in the center of the plate (Crittenden et al. 1995). Plates were sealed with Parafilm and incubated at 18°C , for up to six months. Samples were re-plated to isolate pure cultures, using the same initial media type. Once pure cultures were obtained, they were stored at 4°C for morphological observation and DNA extraction.

To extract total genomic DNA, the Gentra PureGene DNA Extraction Kit (Qiagen) was used. Small quantities (3mm^2) of the pure active culture were removed from the media and 600 μl of cell lysis solution and 10 μl proteinase K were added. Samples were vortexed for 60 seconds and incubated at 55°C overnight. Ammonium acetate (100 μl 7.5M) was added to room temperature samples, vortexed for 20 seconds, and incubated at 4°C for 5 minutes. The protein pellet left behind after the samples was centrifuged (3 min @ 15000 rpm) and then placed on ice. Isopropyl alcohol (300 μl) was added and mixed, the samples were centrifuged for 5 minutes, and the alcohol discarded.

The resulting DNA pellet was washed with ethanol (300µl, 70%), then dried in the rotovac for 30 minutes before 100µl elution buffer was added. Each sample was then incubated at 55°C for 10 minutes.

The nuclear 18S small subunit rDNA and internal transcribed spacer regions (including 5.8S) were amplified using polymerase chain reactions (PCR) using primers listed in Table 2. Each 25 µL PCR reaction contained the following reagents: 2.5 µL 10X buffer, 0.5 µL 10mM dNTPs, 4.125 µL 15 mg/mL BSA, 0.2 µL Taq polymerase, 14.625 µL sterile water, 1.0 µL diluted template DNA, and 0.5 µL of each forward and reverse primer. PCR cycling reactions were performed for primer sets nssu131/ NS4 and ITS1/ITS4 using the following parameters: 5 minutes at 95°C; 40 cycles of 45 seconds at 95°C, 1 minute at 60°C, 2 minutes at 72°C; and 10 minutes at 72°C. PCR thermocycling conditions for NS3 and NS6 were: 5 minutes at 95°C, 30 seconds at 95°C, 30 seconds at 60°C to 50°C, 1°C increments, 1 minute 72°C; 25 cycles of 30 seconds at 95°C, 30 seconds at 50°C , 1 minute at 72°C; and 5 minutes at 72°C. Products of the PCR reactions were cleaned up using the enzymatic reactions SAP-EXO and prepared for cycle sequencing using a Big Dye Terminator Kit (10µL reactions: 2.0 µL of BigDye buffer, 0.5 µL of primer, 6.5 µL of sterile water, and 1.0 µL of PCR product) following the manufacturer's instructions with the following settings: 2 minutes at 96°C; 34 cycles of 20 seconds at 96°C, 20 seconds at 50°C, 4 minutes at 60°C. Samples were sequenced using ABI 3500 XL, with alignments achieved in Geneious 11.1.4 (Kearse et al. 2012), sequences were manually checked and trimmed, and finally BLAST searches performed using the NCBI GenBank database (Altschul et al. 1990) for taxonomic identification.

Molecular Assessment

In addition to extracting DNA from pure cultures as listed above, environmental fungal samples were collected for molecular analysis and DNA extraction done via the CTAB method (Porebski et al. 1997). An amended CTAB protocol was chosen to help increase the success of extraction when plant chemicals such as polysaccharides, terpenes, and aldehydes may be present in the fungal samples. Cetyl trimethylammonium bromide (600 μ L CTAB 2X) was added to approximately 50 fungal ascocarps collected from each individual tree sampled. These samples were bead beat for 2 minutes, then incubated at 65°C for one hour. The rest of the protocol follows Porebski et al. (1997) with the addition of a 15-minute speed vac to dry the DNA pellet before re-suspending in Tris-Cl. Template DNA was diluted (1:10 and 1:100) depending on the intensity of the band.

DNA was amplified using primer sets and PCR conditions listed previously. Amplified products were cloned and amplified using TOPO TA Cloning Kit and Transform ONE-SHOT TOP10 competent cells (Invitrogen). For cloning cycles, A and B, competent cells with inserted vectors were plated on LB media plates + kanamycin (50 μ g/mL), products from cloning cycles C – F were grown on LB plates + ampicillin (50 μ g/mL). Products of the PCR reactions were cleaned up using SAP-EXO and prepared for cycle sequencing using Big Dye Terminator (10 μ L reactions) using the manufacturer's instructions. Samples were sequenced using ABI 3500 XL, with alignments achieved in Geneious 11.1.4 (Kearse et al. 2012) and subjected to BLAST searches using the NCBI database (Altschul et al. 1990).

Table 2. Primers used for PCR amplification and cycle sequencing reactions.

Targeted region	Primer name	Sequence	Position and orientation	Reference
SSU rDNA	nssu131	5'-CAGTTATCGTTTATTTGATAGTACC-3'	107-131	(Kauff & Lutzoni 2002)
	NS4	5'-CTTCCGTCAATTCCTTTAAG-3'	1150-1131	(Kauff & Lutzoni 2002)
	NS3	5'-GCAAGTCTGGTGCCAGCAGCC-3'	553-573	(Innis et al. 2012)
	NS6	5'-GCATCACAGACCTGTTATTGCCTC-3'	1436-1413	(Innis et al. 2012)
ITS and 5.8S	ITS 1	5'- TCCGTAGGTGAACCTGCGG -3'	1769-1787 (ssu)	(Innis et al. 2012)
	ITS 4	5'- TCCTCCGCTTATTGATATGC-3'	60-41 (lsu)	(Innis et al. 2012)

Phylogenetics

Mycologists once debated the value of molecular versus morphological data. Most research now demonstrates the empirical value of both and the synthesis of research that plots morphological characters along an evolutionary timeline is referred to as phylogenetic character mapping (Mitchell et al. 1995). Traditionally, taxa were grouped based on characters such as the shape and size of the ascocarp, ascus, and ascospore, along with dispersal technique, presence of secondary metabolites, and presence of an anamorph/teleomorph (Frisvad 1998; Guarro et al. 1999). As molecular mycology and phylogenetics advance together, the number of species revisions and new species will increase dramatically, and complex multi loci analyses using Maximum Likelihood and Bayesian methods will become standard practice in the new age of fungal taxonomy and systematics.

Bayesian inference of phylogeny is a powerful tool for analyzing large datasets and complex substitution models. These statistical methods use posterior probabilities that can estimate which phylogeny is the best (Huelsenbeck et al. 2001). Using Bayes's Theorem independently is almost analytically impossible due to computational time, however employing the statistical methods of Markov chain Monte Carlo can help solve complex evolutionary problems. The Markov chain Monte Carlo algorithm samples the tree space by proposing new trees and evaluating their probabilities; eventually these chains will converge in high posterior probability (Mau et al. 1999; Huelsenbeck et al. 2001; Larget and Simon 1999). The samples the algorithm records before the chains converge are usually discarded, which is referred to as the burn-in (Nascimento et al. 2017). Bayesian inference is a powerful tool because unlike Maximum Parsimony,

which measures the tree with the fewest number of changes, Bayesian analysis with MCMC considers many different topologies and calculates support for the probability of their occurrence (Huelsenbeck et al. 2001).

Robergea albicedrae was compared to 36 ascomycetes (Table 3) along a partial 18S rDNA region and 23 other ascomycetes (Table 4) along the ITS 1 and 2 region. Sequence data from the 18S SSU and ITS regions were retrieved from GenBank (Clark et al. 2016) and several species within Stictidaceae and Ostropales are represented. These rDNA sequences were chosen to create topologies in which relationships between OTUs could be determined. The 18S SSU region resulted in 269 bp after alignment. *Phoma* sp. was set as the outgroup and rooted so the outgroup would be a monophyletic sister group to the ingroup. This was set as the default for all the trees produced when comparing the 18S region. Nucleotide sequences were imported into Geneious 11.1.4 (Kearse et al. 2012) and aligned using CLUSTALW 2.1 (Larkin et al. 2007).

The ITS region (including 5.8S) was also compared, looking at species in and closely related to the family Stictidaceae (23 individuals sampled). The root for these trees was *Trullula melanchlora*, which was set as the outgroup and rooted so it would be a monophyletic sister group to the ingroup. Sequence data for all taxa sampled (except *R. albicedrae*) were retrieved from GenBank (Clark et al. 2016). These 23 ITS rDNA sequences were chosen to create a topology in which relationships between OTUs could be determined. The ITS region included ITS 1 and 2 which span the 5.8S gene and resulted in 351 bp after alignment.

Analyses for both loci (analyzed individually) included searching for the most parsimonious trees using PAUP* 4.0a (Swofford 2017) to conduct neighbor joining and

maximum likelihood analyses (Felsenstein 1981; Tateno et al. 1994). Support for each tree was measured with bootstrap analysis (Felsenstein 1985; Nei and Miller 1990; Roff and Preziosi 1994). When multiple trees were determined to be most parsimonious, strict consensus trees were created for each type of analysis (Anderberg and Tehler 1990; Maddison 1991; Page 1993). Transition and transversion rates were calculated (Hasegawa et al. 1991; Purvis and Bromham 1997; Ina 1998; Strandberg and Salter 2004) and the appropriate nucleotide substitution model was applied, based on ranked changes in Akaike Information Criterion (AIC) (Akaike 1979; Burnham and Anderson 2004).

In order to determine the best nucleotide substitution model, jModeltest2 (Guindon et al. 2003; Darriba et al. 2012) on XSEDE using the CIPRES (Miller et al. 2010) platform was used based on ranked Akaike Information Criterion. A bootstrap consensus neighbor joining tree was produced using the general time-reversible model with a gamma distribution and bootstrap resampling of 1000 replicates.

Bayesian analysis was performed using MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The Markov chain Monte Carlo (MCMC) algorithm ran two runs of 4 chains each. Chains were sampled every 1,000 trees for 5,000 generations with a burn-in fraction value of 0.25 and a temperature of 0.2. The approximated posterior probabilities are presented on each tree branch as support for that branch according to conditioned observations.

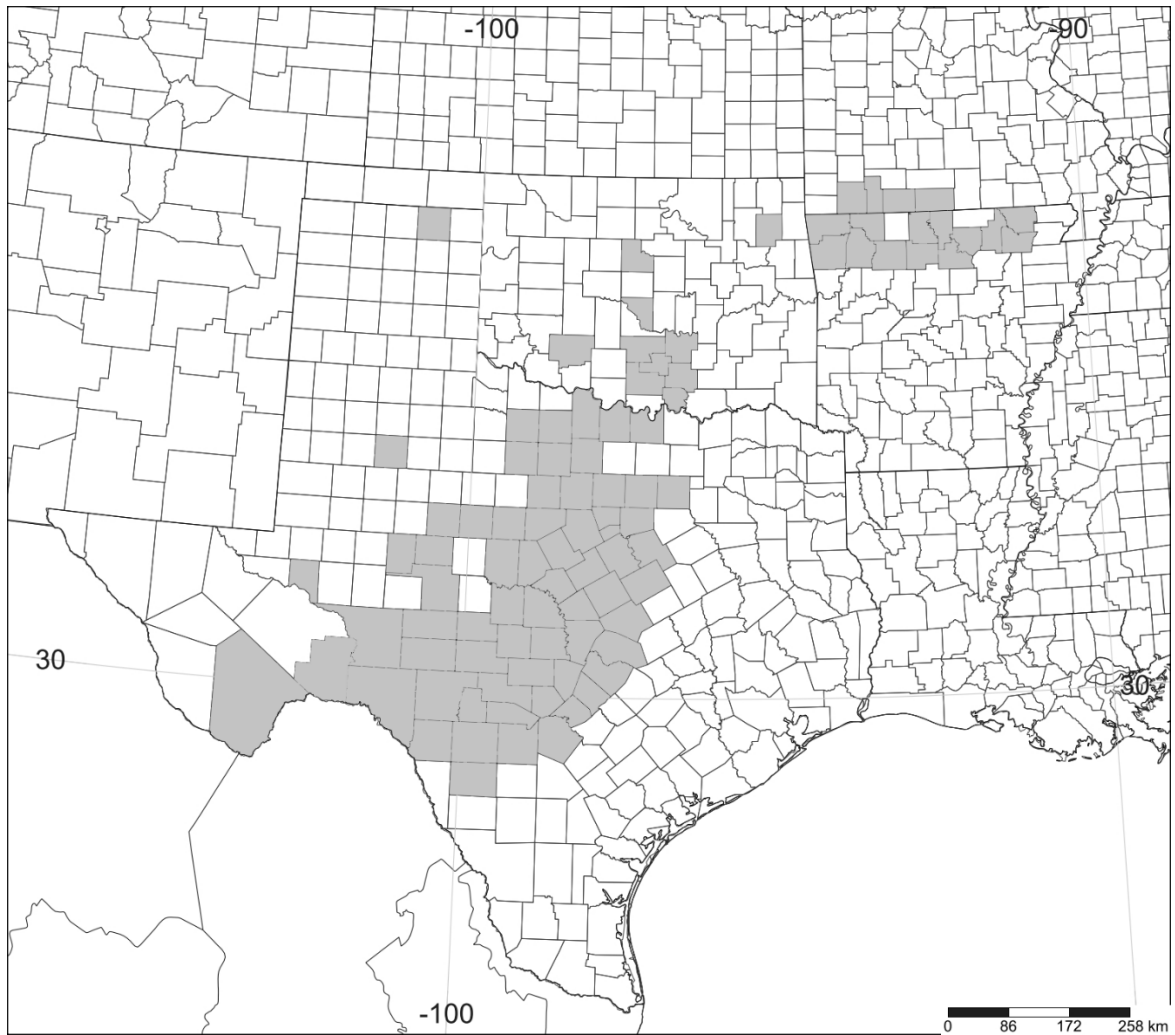


Figure 1. Distribution of *Juniperus ashei* in the United States based of USDA Forest Service data (Thompson et al. 1999).

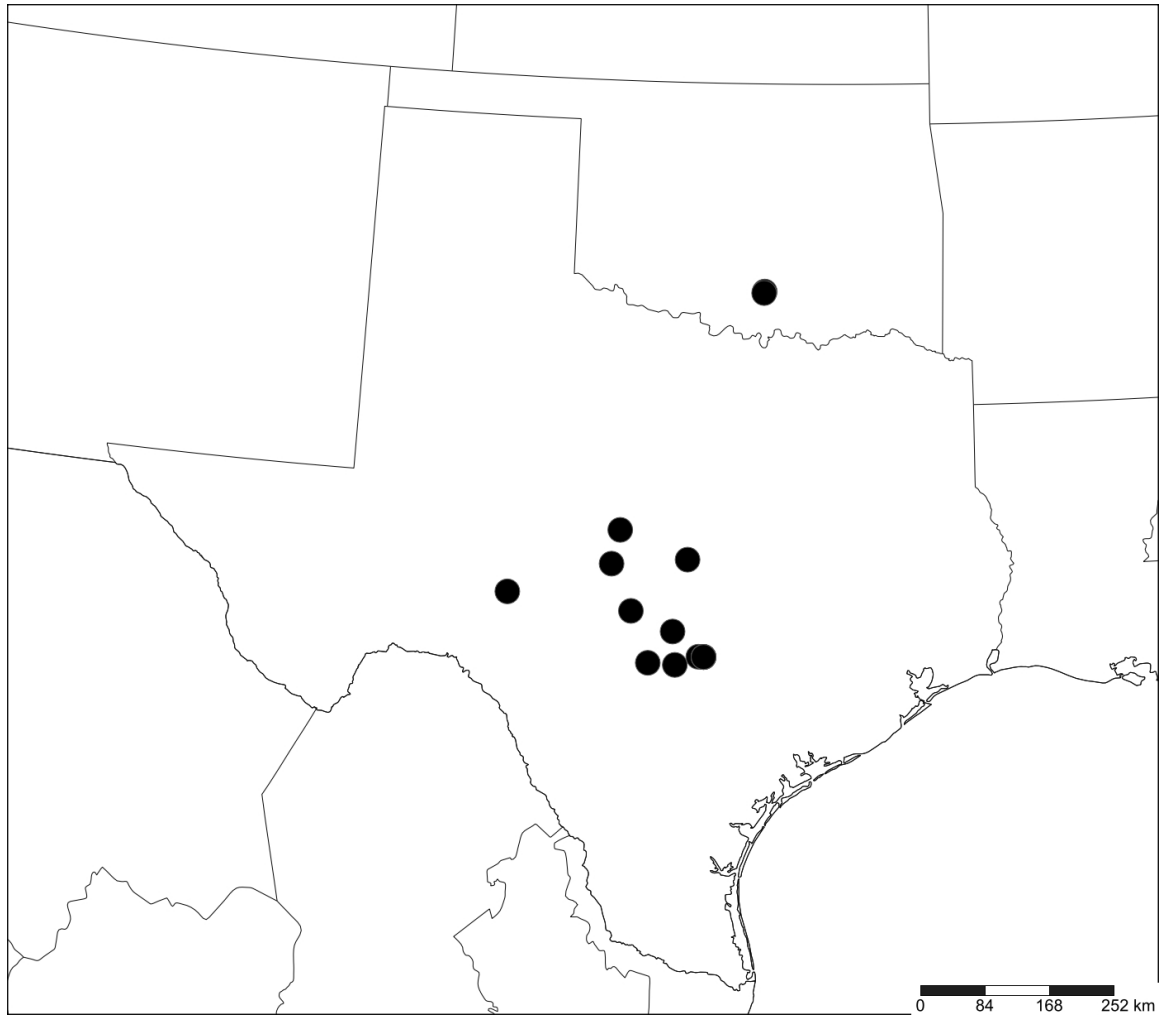


Figure 2. Map of sample sites across the Edwards Plateau in Texas (USA), west to Sonora, TX, and north to southern Oklahoma. Twelve individual sites resulted in 22 fungal samples for molecular analysis and 12 voucher specimens of *J. ashei*.

Table 3. Species taxonomic information and accession numbers from GENBANK for 18S phylogenetic trees.

Species	Order	Family	Accession
<i>Bactrodesmium longisporum</i>	Helotiales	Hyaloscyphaceae	MN335225
<i>Epiglia gloeocapsae</i>	Helotiales	Helotiaceae	EU940055AF2
<i>Micarea denigrata</i>	Lecanorales	Pilocarpaceae	KJ766750
<i>Mniaecia nivea</i>	Leotiales	Mniaeciaceae	EU940042
<i>Lichenodium sirosiphoideum</i> 1	Lichenales	Lichenaceae	MK225517
<i>Lichenodium sirosiphoideum</i> 2	Lichenales	Lichenaceae	MK225516
<i>Conotrema populorum</i>	Ostropales	Stictidaceae	U86582
<i>Acarosporina microspora</i>	Ostropales	Stictidaceae	AY584667
<i>Cyanodermella viridula</i>	Ostropales	Stictidaceae	U86583
<i>Cryptodiscus cladoniicola</i> 1	Ostropales	Stictidaceae	KY661694
<i>Cryptodiscus cladoniicola</i> 2	Ostropales	Stictidaceae	KY661695
<i>Cryptodiscus galaninae</i>	Ostropales	Stictidaceae	KY661701
<i>Gyalidea hyalinus</i>	Ostropales	Gomphillaceae	DQ973023
<i>Lepolichen coccophorus</i>	Pertusariales	Coccotremataceae	AF274110
<i>Phoma</i> sp.	Pleosporales	Didymellaceae	MH051122
<i>Rhopalophora clavispora</i> 1	Sclerococcales	Sclerococcaceae	NG_061246
<i>Rhopalophora clavispora</i> 2	Sclerococcales	Sclerococcaceae	KX537772
<i>Cylindroconidiis aquaticus</i>	Sclerococcales	Sclerococcaceae	MH236580
<i>Xanthomendoza ulophyllodes</i> 1	Teloschistales	Teloschistaceae	AM495018
<i>Xanthoria borealis</i>	Teloschistales	Teloschistaceae	AJ535292
<i>Caloplaca</i> sp.	Teloschistales	Teloschistaceae	DQ641413
<i>Xanthomendoza mendozae</i>	Teloschistales	Teloschistaceae	AM494994
<i>Teloschistes hosseusianus</i>	Teloschistales	Teloschistaceae	JQ301632
<i>Teloschistes hosseusianus</i>	Teloschistales	Teloschistaceae	AM495013

Table 3. Continued

Species	Order	Family	Accession
<i>Teloschistes</i> cf.	Teloschistales	Teloschistaceae	AF088252
<i>Niorma chrysophthalma</i> 1	Teloschistales	Teloschistaceae	KJ766804
<i>Niorma chrysophthalma</i> 2	Teloschistales	Teloschistaceae	JQ301629
<i>Megalospora tuberculosa</i> 1	Teloschistales	Megalosporaceae	JQ301628
<i>Caloplaca chilensis</i>	Teloschistales	Teloschistaceae	JQ301608
<i>Wiesneriomyces conjunctosporus</i>	Tubeufiales	Wiesneriomycetaceae	KJ425442
<i>Wiesneriomyces laurinus</i>	Tubeufiales	Wiesneriomycetaceae	KJ425447
<i>Wiesneriomyces javanicus</i>	Tubeufiales	Wiesneriomycetaceae	MH985633

Table 4. Species taxonomic information and accession numbers from GENBANK for ITS phylogenetic trees.

Species	Order	Family	Accession
<i>Trullula melanochlora</i>	-	-	KP004459
<i>Phacidiella</i> sp. DTO 305-C5	Helotiales	Phacidiella	KX147603
<i>Phacidiella</i> sp. DTO 305-C4	Helotiales	Phacidiella	KX147602
<i>Phacidiella eucalypti</i>	Helotiales	Phacidiella	EF110620
<i>Phacidiella eucalypti</i> strain	Helotiales	Phacidiella	EF110617
<i>Schizoxylon gilenstamii</i> 9490	Ostropales	Stictidaceae	MG283967
<i>Schizoxylon gilenstamii</i> 9493	Ostropales	Stictidaceae	MG281968
<i>Schizoxylon gilenstamii</i> 9496	Ostropales	Stictidaceae	MG281969
<i>Carestiella socia</i> 1	Ostropales	Stictidaceae	AY661682
<i>Carestiella socia</i> 2	Ostropales	Stictidaceae	AY661687
<i>Acarosporina microspora</i>	Ostropales	Stictidaceae	DY782834
<i>Stictis radiata</i> ICMP	Ostropales	Stictidaceae	MK547089
<i>Stictis radiata</i> MW6493	Ostropales	Stictidaceae	AY527309
<i>Stictis radiata</i> isolate	Ostropales	Stictidaceae	AY527308
<i>Robergea cubicularis</i>	Ostropales	Stictidaceae	KY611899
<i>Conotrema urceolatum</i>	Ostropales	Stictidaceae	AY661686
<i>Stictis urceolatum</i>	Ostropales	Stictidaceae	HQ650601
<i>Stictis brunnescens</i>	Ostropales	Stictidaceae	MG281970
<i>Schizoxylon albescens</i> 1	Ostropales	Stictidaceae	HQ287299
<i>Schizoxylon albescens</i> 2	Ostropales	Stictidaceae	HQ287303

III. RESULTS

In Situ Coverslip Observations

Coverslips were collected and photographed every three months for 17 months after being attached to Ashe juniper trees, resulting in 108 coverslips collected. The coverslips showed significant colonization by fungi and algae, along with a myriad of spores, pollen, invertebrates, and dust. Since colonization and deposition of organisms occurred on both sides of the coverslip, after viewing with a dissecting scope the side with the lesser amount of deposition was wiped clean with DI water and a Kim-wipe. In some cases when growth on the surface was minimal, both surfaces were viewed by focusing and photographing one side, then refocusing and viewing at a deeper plane of focus.

Stages of development depended on length of time after initial placement. Figure 3 shows hyphal growth from March 2018 to March 2019. Figures 3A, B, and C show hyphal growth on coverslips harvested at three different intervals. Figures 3F and G show fungal hyphae growing with algae. Growth of fungi and deposition of dust and spores also seemed to correspond to the lines of the mesh and burlap grids they were placed on. Figure 4 shows several types of algae and a few cyanobacteria found colonizing the bark of Ashe juniper, the most common being *Westella* sp. and *Trebouxia* sp. Many times, fungal hyphae could be seen growing among the algal cells or in proximity to them (Figure 4B). Figure 4H shows a small piece of juniper bark, with small clumps of green algae present along with a few strands of very thin fungal hyphae.

Calcium oxalate was found on the coverslips as seen in Figure 5F, along with copious amounts of pollen, most notably that of *J. ashei* (Figure 5D). Small pieces of

Ashe juniper bark were found on many of the coverslips. Often, they were too thick to observe with the light microscope, but thinner sections could be seen supporting algal growth (Figure 5C), calcium oxalate residue, and highly pigmented areas that may correspond to fungal fruiting bodies (Figure 5B). Every coverslip also had numerous plant trichomes (Figure 5A, F). Figure 5G is an image of an unknown organism found on one coverslip.

Fungal spores present on the coverslips were numerous and diverse. Figure 6 illustrates the most common fungal spores found and demonstrates the great diversity in shape, size, color, and growth form. Most appear to be common molds and plant pathogens such as *Fusarium* sp., *Aspergillus* sp., *Beltrania* sp., *Alternaria* sp., *Pithomyces* sp., along with others. Other fungal spores found belonged to the species of interest, *R. albicedrae*. Figure 7 illustrates the multi-septate spores that are typically greater than 200 μm in length and 1-2 μm wide. Sometimes the spore was observed to be breaking into segments along septations. Spores of *R. albicedrae* were not consistently found on the coverslips. The coverslips collected late in the experiment had a higher abundance of these spores. Other coverslips included hyphae with conidia (Figure 6E), germinating spores surrounded by green algae and some hyphal growth (Figure 3F), and two distinctly different species of fungi displaying hyphal growth on the coverslips, one in connection with algae (Figure 3G) and one without an associated alga (Figure 3H).

There was an interesting array of animal life present on the coverslips. Coverslips that contained these organisms were often hard to photograph because the subjects were moving (mites, spiders, and protists). Figure 8 illustrates a nematode (8A) and tardigrade (8C) also parts of invertebrates such as webs, wing scales, appendages, and antennae (8B,

8D), were also commonly encountered.

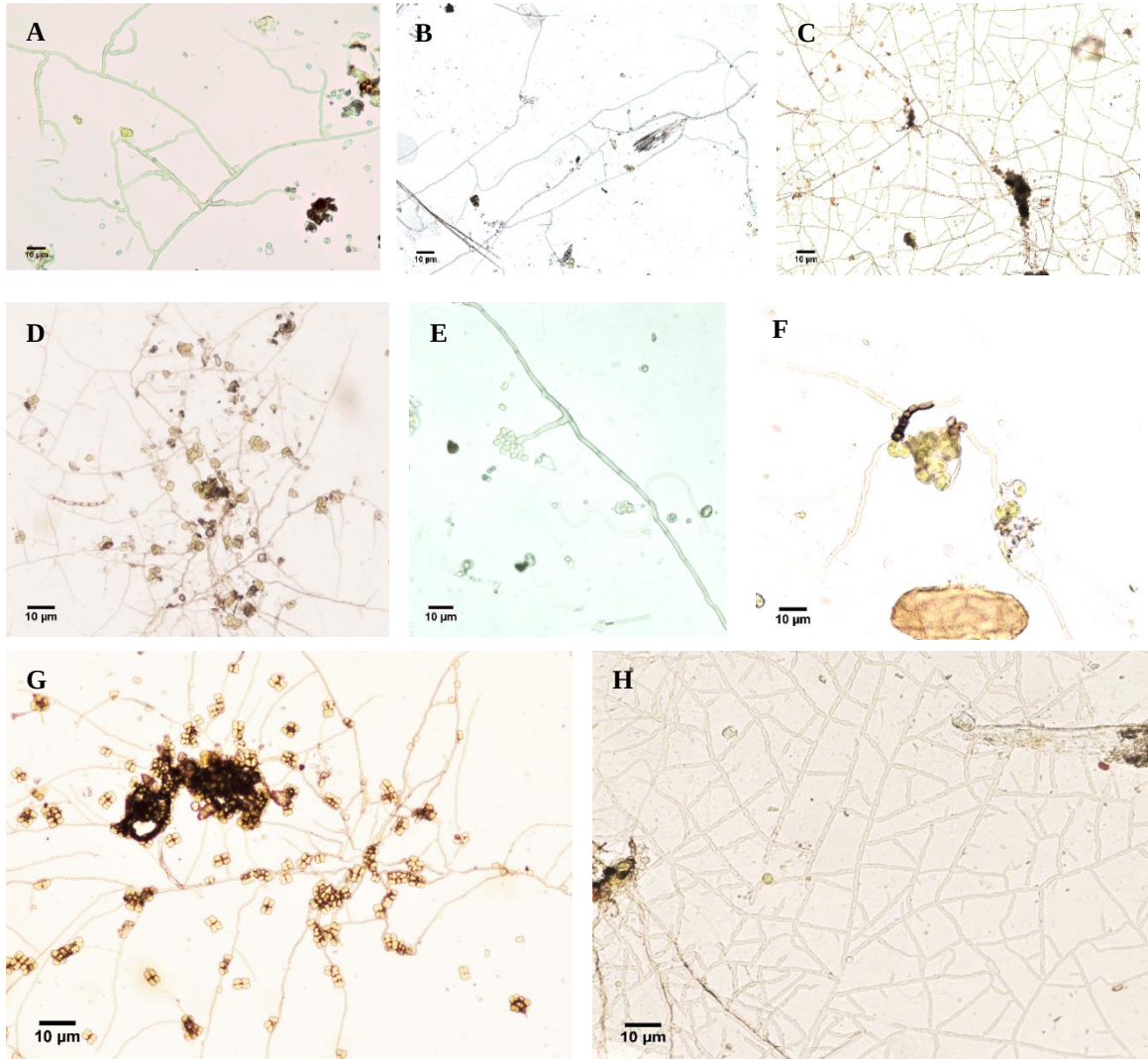


Figure 3. Fungal mycelium and algae growing on plastic coverslips attached to *J. ashei* trees. A. harvested March 2018; B. harvested September 2018; C. harvested February 2019; D. harvested March 2019; E. *Cladosporium* sp. hyphae with conidia; F. germinating fungal spore surrounded by green algae and some hyphal growth; G. mycelial growth with interspersed algae (clumps forming at sites where there is an increase in debris); H. mycelial growth of unknown fungus.

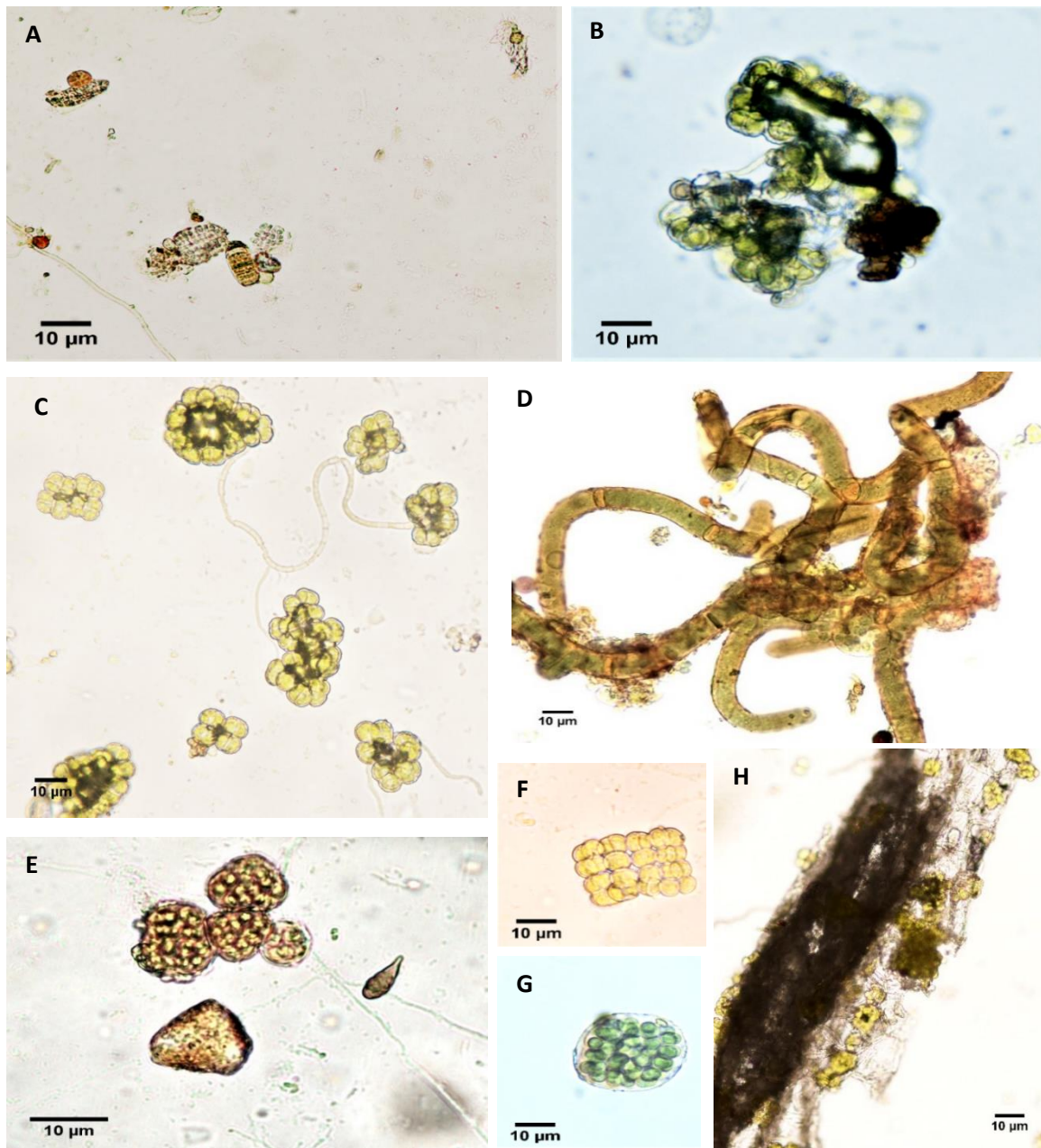


Figure 4. Algae and cyanobacteria found growing on plastic coverslips attached to *J. ashei* trees. The genera listed are possible identifications based on the University of New Hampshire PhytoKey. A. *Merismopedia* sp.; B, C. *Westella* sp.; D. *Scytonema* sp.; E. *Trebouxia* sp. with small *Alternaria* sp. spore; F. *Crucigenia* sp.; G. *Trebouxia* sp.; H. green alga colonizing bark of *J. ashei*.

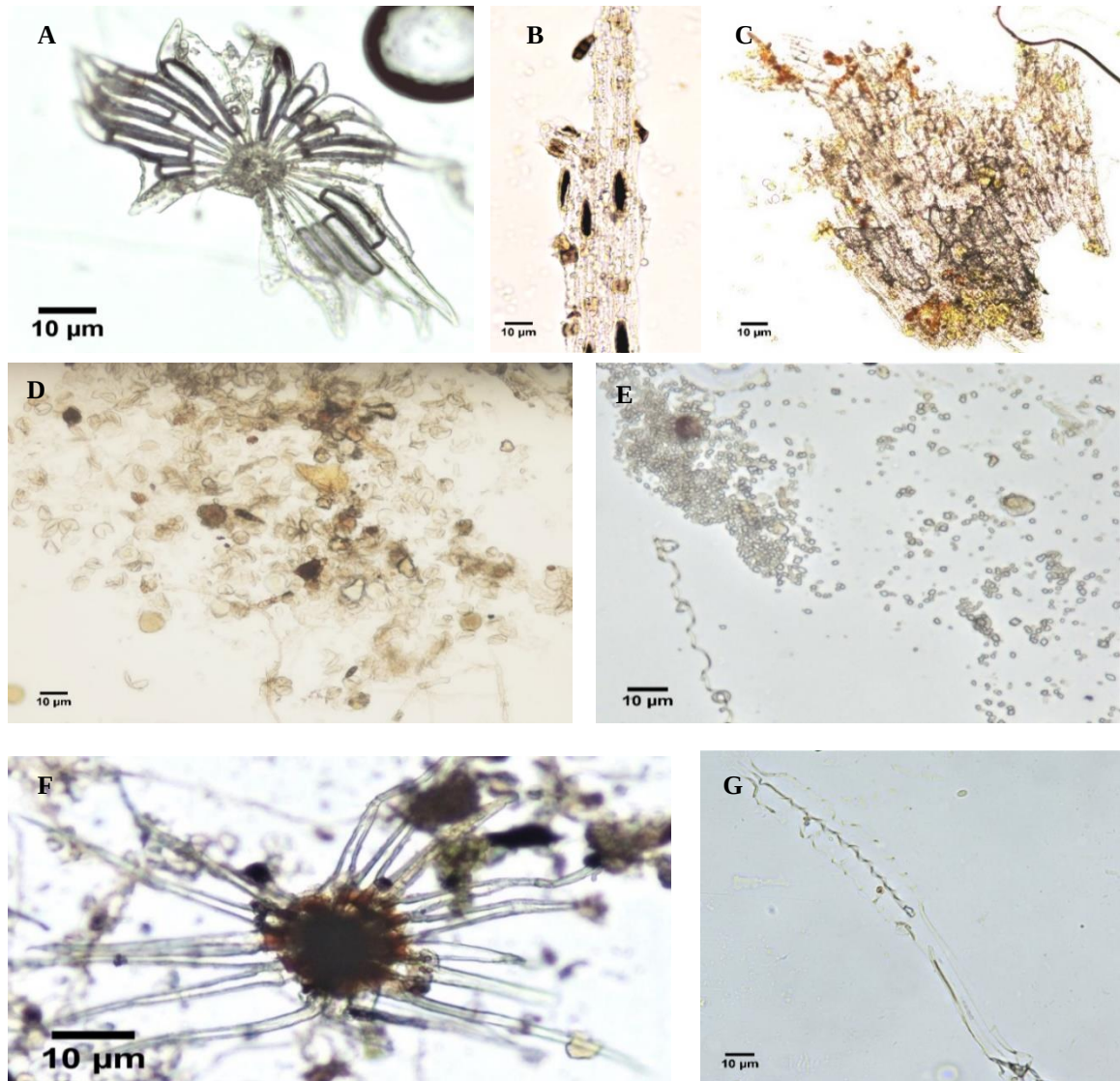


Figure 5. Plant tissues and residues found deposited on plastic coverslips attached to *J. ashei* trees. A. plant trichome; B. thin sliver of *J. ashei* bark showing darkening of the plant cells; C. *J. ashei* bark colonized by green algae and some calcium oxalate present; D. *J. ashei* pollen; E. calcium oxalate crystals; F. plant trichome; G. unknown organism.

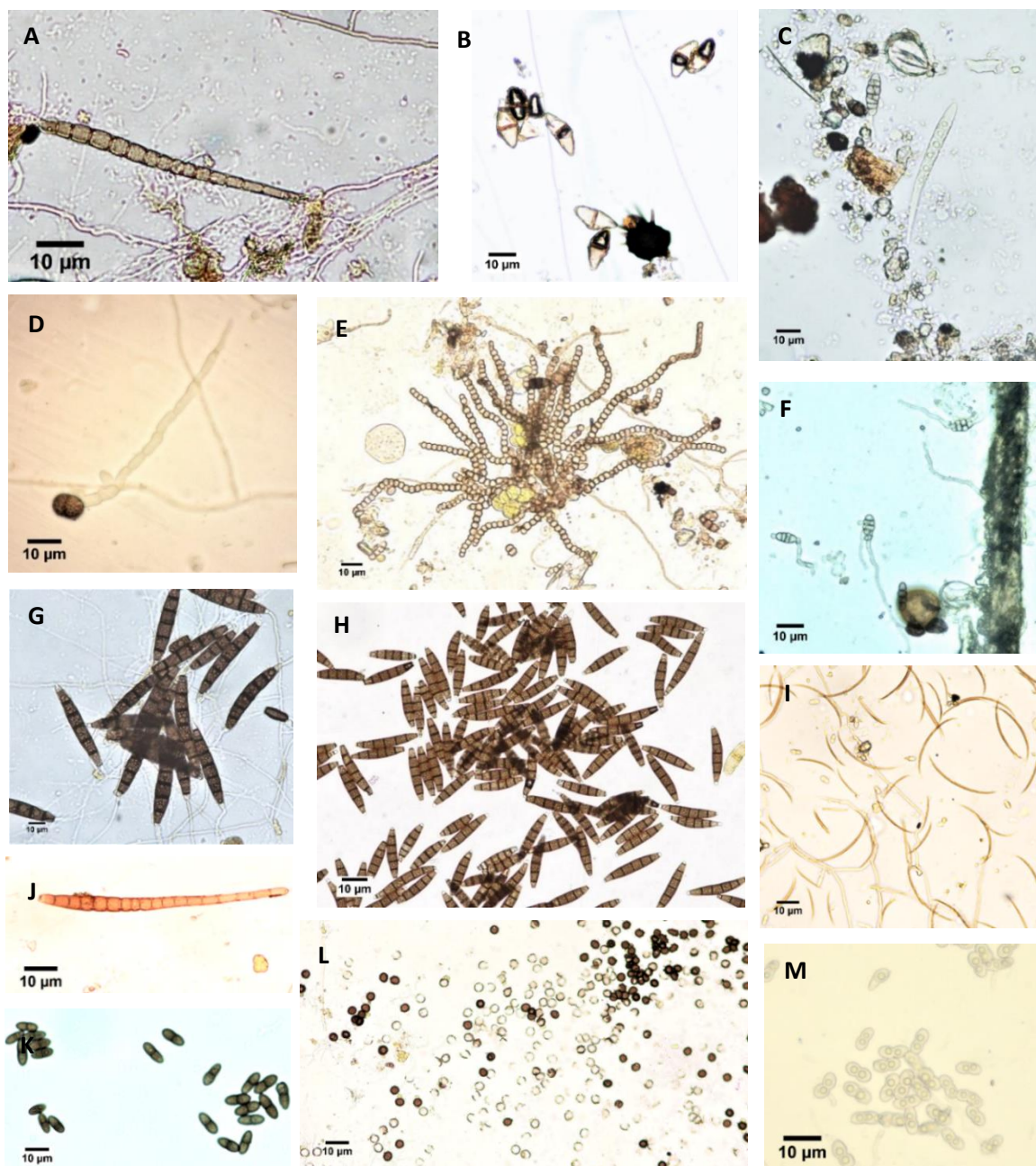


Figure 6. Fungal spores found growing on plastic coverslips attached to *J. ashei* trees. A. unknown fungal spores; B. *Beltrania* sp.; C. *Alternaria* sp.; D. germinating *Epicoccum* sp. spore; E. unknown fungal spores; F. *Alternaria* sp.; G, H. *Bipolaris* sp.; I. *Fusarium* sp., J. unknown fungal spores; K. *Didymosphaeria* sp., L. *Aspergillus* sp., M. unknown fungal spores.

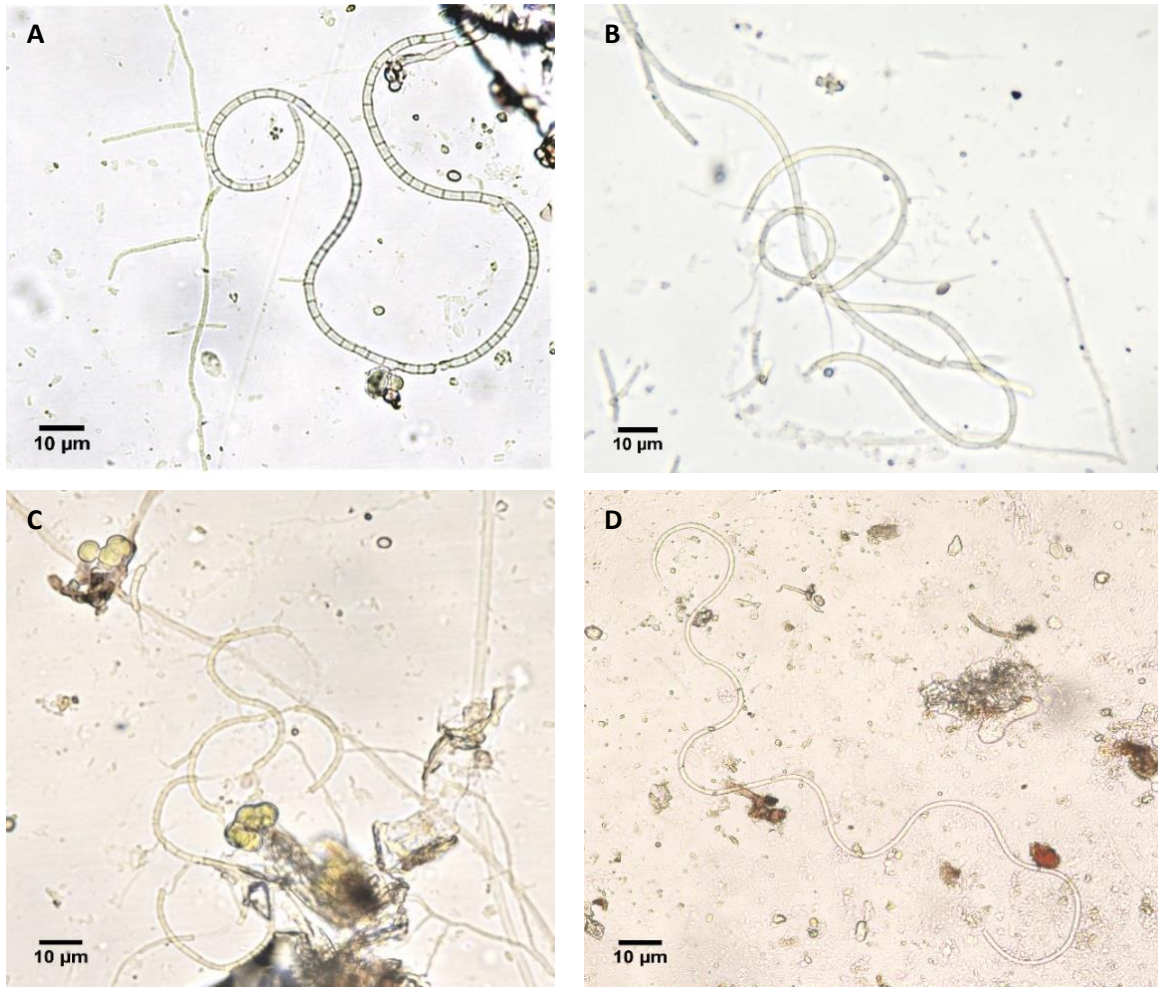


Figure 7. Spores of *Robergea albicedrae*. The spores are multi-septate, over 200 µm in length. A. intact spore; B. spore breaking into segments along septations; C. germinating spore; D. intact spore.

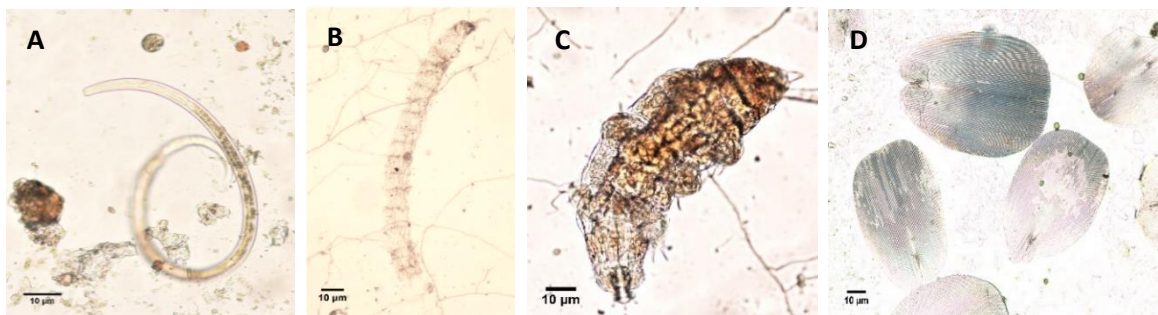


Figure 8. Animal life found on plastic coverslips attached to *J. ashei* trees. A. nematode; B. invertebrate appendage; C. tardigrade; D. lepidopteran wing scales.

Anatomical Observations

Macroscopic images of fungal growth on Ashe juniper were obtained from fresh collections. Figure 9 shows the three growth forms of the fungus: growing on dead, decorticated branches (completely devoid of bark) usually 5.0 mm or less in diameter; growing on small living and dead branches usually between 5.0 mm - 5.0 cm in diameter; and growing on the bark of the main trunk. When the fungus is growing on the larger branches, it is usually dominating one side of the branch. On the bark of the main trunk, the fungus is present on the surface only; if the bark is peeled off, the pruina, perithecium, and hyphae are not present in the wood cells under the strips of bark. Images 9E and 9H show the diversity of lichens present, interspersed among *R. albicedrae*.

Fresh samples cut by hand with a razor blade and viewed by light microscope proved too thick to get good images. Often the bark and outer layers of wood tissue (and fungal tissue) would simply dissolve when water was added to the wet mount. Due to this, samples were preserved in FAA, embedded in paraffin, thin sectioned, and stained. This procedure was particularly rough on the specimens, and any algal growth and some hyphal growth was lost during the staining procedure. Safranin stains chitin and cellulose, and in the cross sections those structures are bright pink/red. Figure 10A shows a cross-section of a perithecium of *R. albicedrae*, the arrow indicating damage to the wood cells at the surface. Figure 10B shows a cross-section of a single ascus containing 8 filiform spores. Figures 10C and 10D show a longitudinal section of a perithecium. In Figure 10D, long filiform spores that have been stained with safranin are visible; interspersed between these ascospores are lighter stained paraphyses.

Figure 11 shows samples also stained with safranin and cut in cross section and longitudinal section. In Figures 11A, B, and C early colonization of the wood cells by the fungus is visible. Fungal hyphae are present in the wood cells and along the surface of the wood. Figure 11D shows strands of fungal hyphae growth, while Figure 11E shows brown stained fungal hyphae within individual wood cells. Figure 11F shows an immature perithecium and fungal growth can be seen in the wood cells surrounding the perithecium.

Slide preparations stained with trypan blue/aniline blue and WGA are illustrated in Figure 12. Figures 12A-C are the same cross section photographed with illumination. Figure 12B, with the lower light intensity, shows greater contrast between the background and very light paraphyses. The CLSM shows the autofluorescence of the wood cells and a slight fluorescence of the fungal spores, however the paraphyses remain translucent. Figure 12D is a compressed Z-stack image of an unstained surface bark sample, obtained using CLSM; the image highlights the ostiole where spores are released. Figure 12E shows a longitudinal section of a perithecium stained with WGA; the arrow indicates spores that have been pulled out of the perithecium during thin sectioning. Figure 12F is a cross-section of a branch; the bark did not persist during staining, however, the fluorescence of hyphae in cross-section can be seen (arrows) using trypan blue/aniline blue stain.

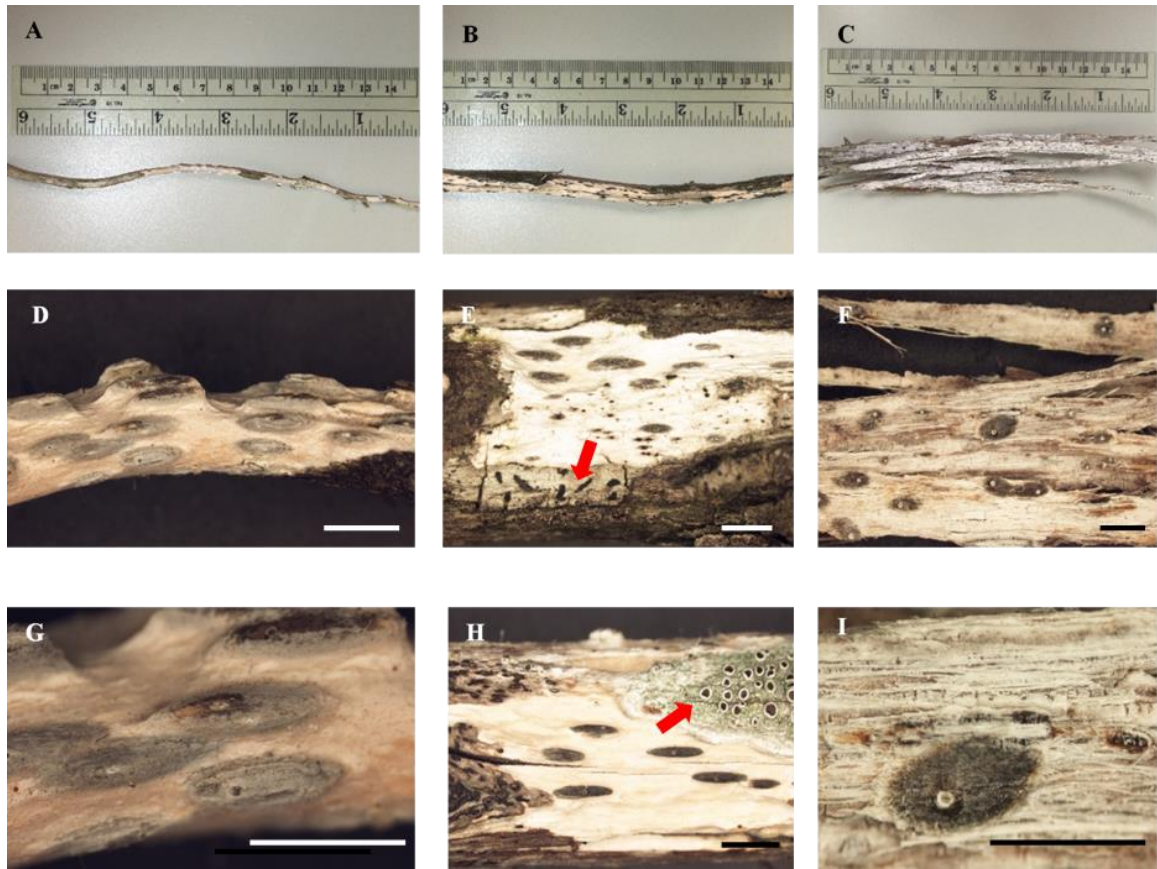


Figure 9. Habit and details of *Robergea albicedrae* on its host plant, *Juniperus ashei*. A. pruina and immersed perithecia on a decorticated dead twig; B. fungal growth on a larger living branch; C. fungal growth on bark from *J. ashei* trunk (living mature tree); D. twig devoid of bark, and several perithecia with associated ostiole; E. perithecium, pruina, and two lichens, (arrows); F. perithecium, pruina, and ostiole; G. twig devoid of bark, and several perithecia with associated ostiole; H. perithecium, pruina, and two lichens, (arrows); I. perithecium, pruina, and ostiole. Scale bar = 2.0 mm.

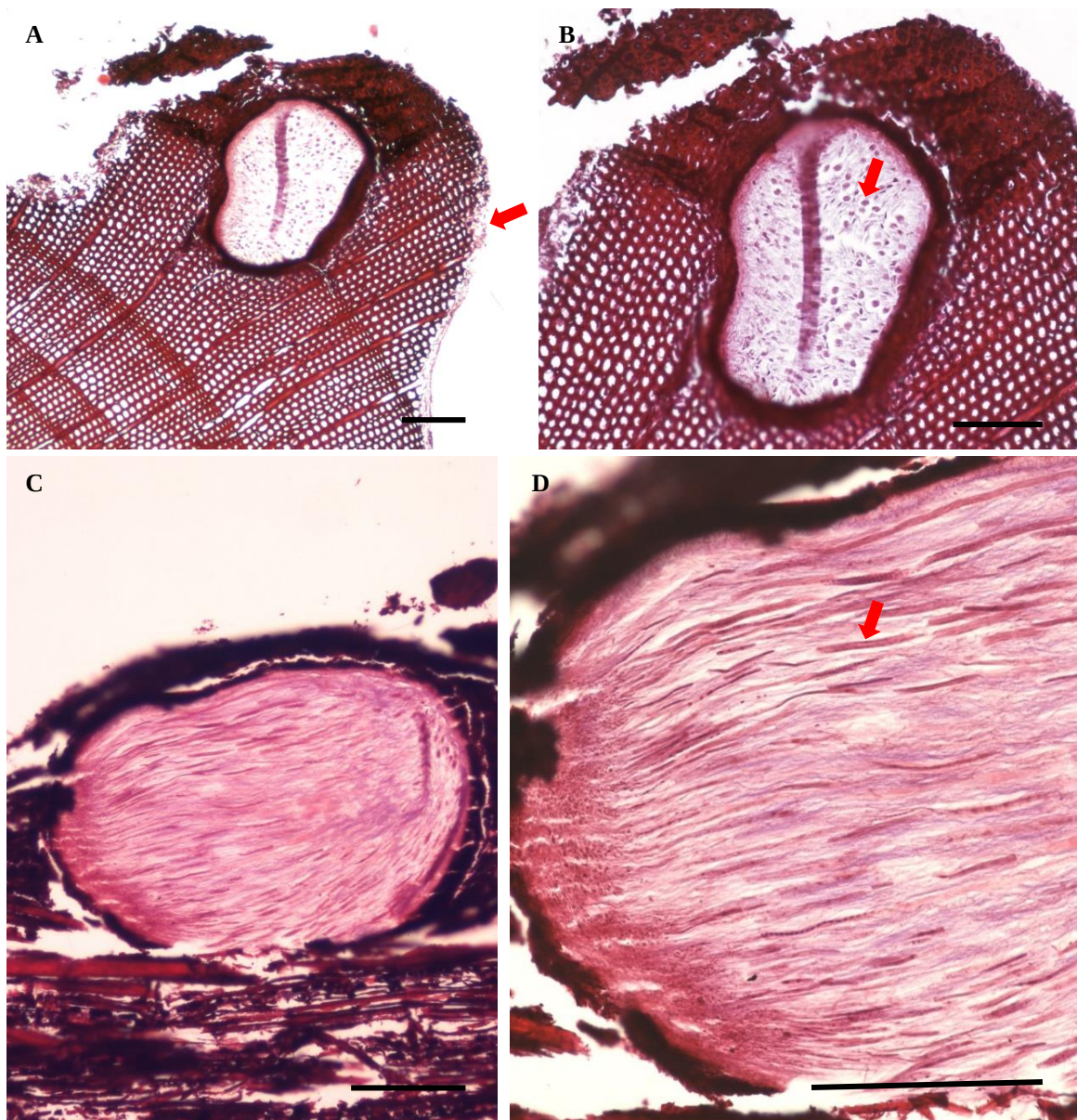


Figure 10. Cross and longitudinal sections of perithecia of *R. albicedrae*. A. Changes in the shape of the wood cells around the perithecium, arrow shows the breakdown of wood cells on the surface of the branch; B. Magnified image of A with an arrow showing a cross section of an ascus containing 8 filiform spores; C. Longitudinal section of perithecium of *R. albicedrae*; D. Longitudinal section showing one of many filiform spores intercalated with paraphyses. Scale bar = 30 μ m.

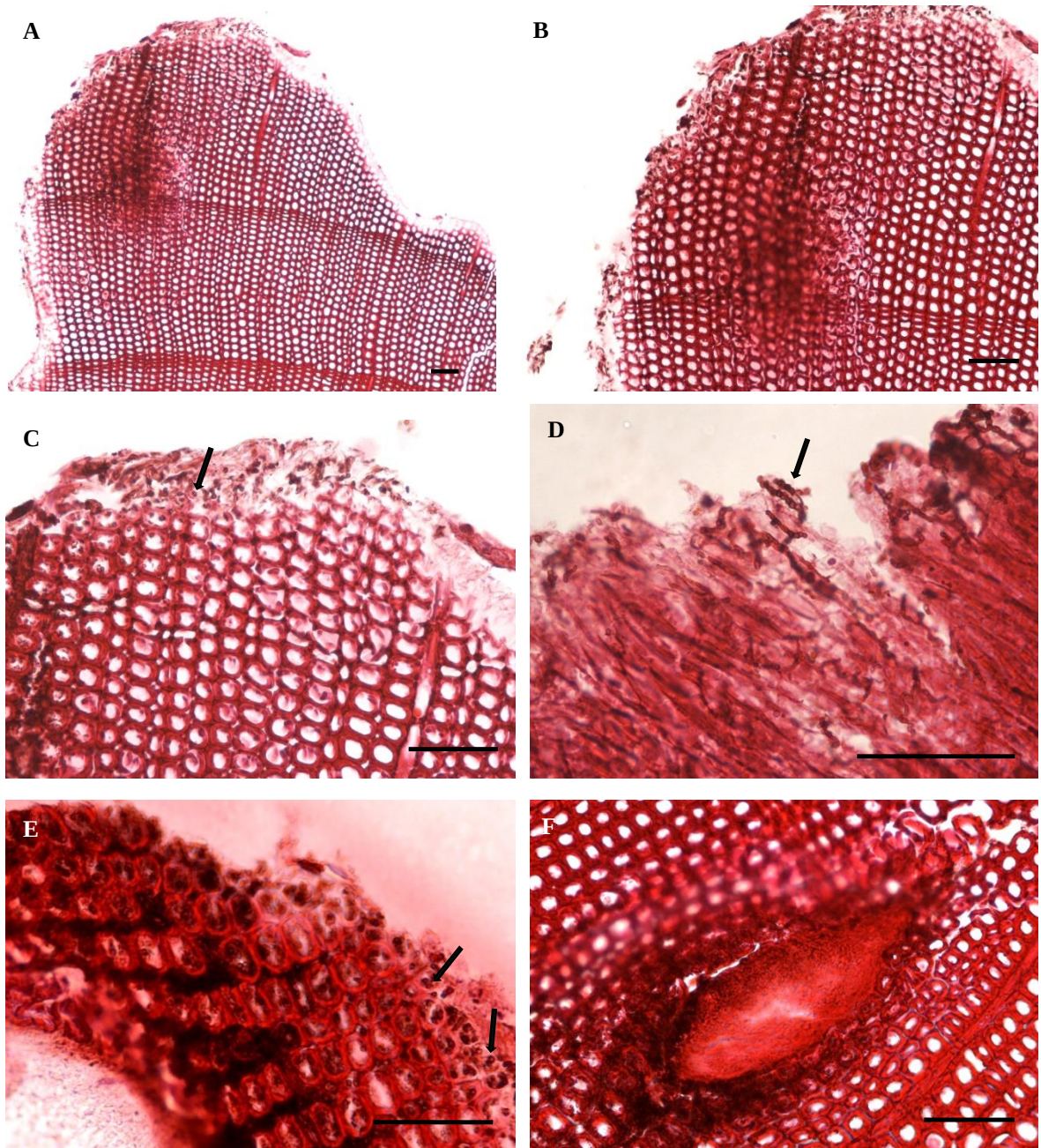


Figure 11. Wood of *J. ashei* stained with safranin illustrating the presence of fungal hyphae. A-C. Slide prep at different magnifications; arrow indicates fungal hyphal growth; D. Longitudinal cross section showing strands of fungal hyphae growth (arrow); E. Wood cells on the surface of a branch, with brown stained fungal hyphae (arrow); F. Immature perithecium; fungal growth can be seen in the wood cells surrounding the perithecium, there are no fungal spores present. Scale bar = 20 μ m.

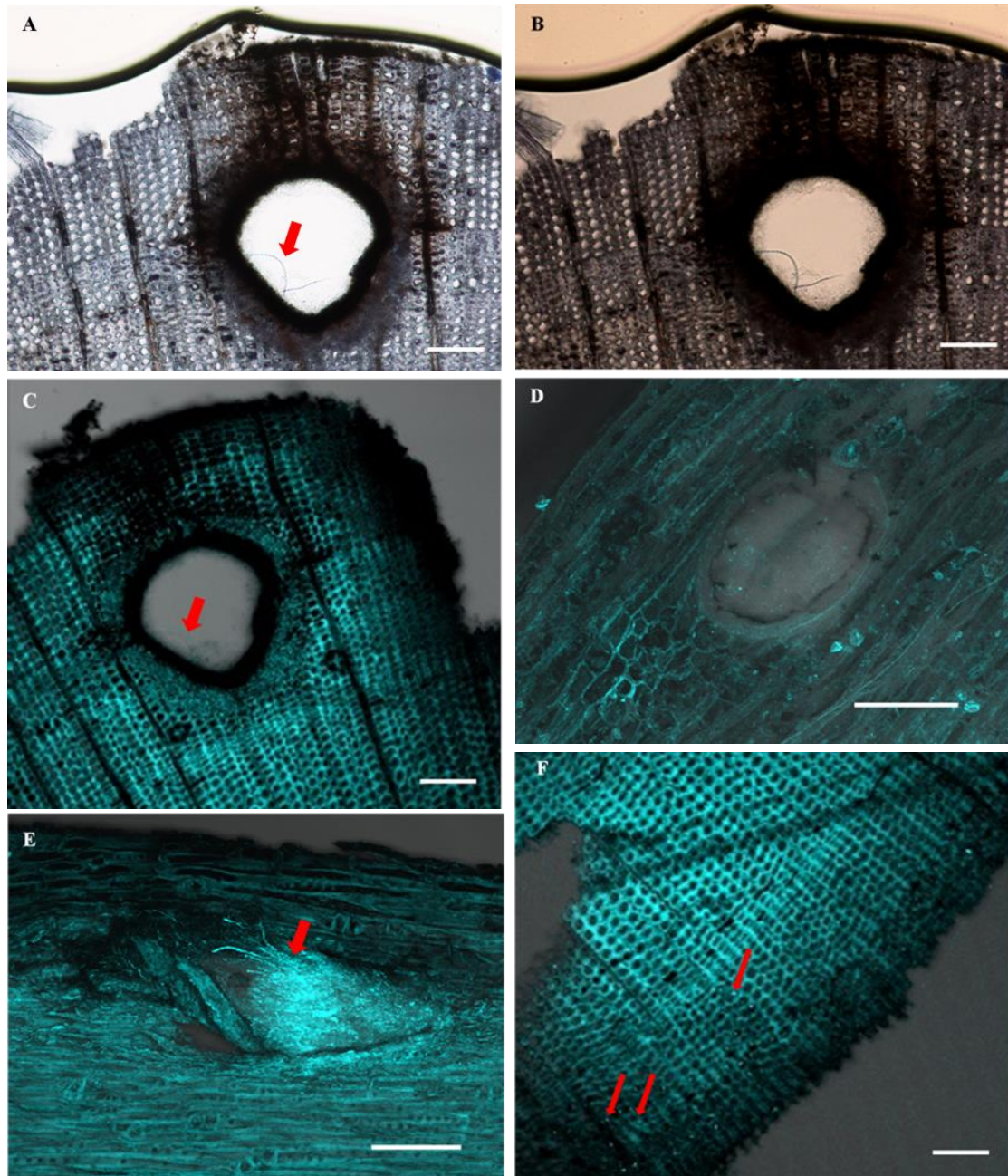


Figure 12. Microscopic images of fungal perithecia, spores, and hyphae of *Robergea albicedrae*. A, B, C, D, F. stained with trypan blue/aniline blue stain; E. Stained with WGA. A. Cross section of perithecium, carbonized wood tissue is visible along with two spores inside the perithecium; B. Same image with lower light for better resolution of spores and paraphyses in the perithecium; C. Same sample under CLSM, the green is the autofluorescence of the wood cells, a slight fluorescence of fungal spores can be detected; D. Unstained compressed Z-stack using CLSM of ostiole; E. Longitudinal section of a perithecium stained with WGA, the arrow indicates spores; F. Cross-section of a branch, the bark did not persist during staining, but the fluorescence of hyphae in cross-section can be seen (arrows) using trypan-blue/aniline stain. Scale bar = 30 μ m.

Pruina Composition Test

Infrared spectra were obtained for each of the three trees sampled. Samples were obtained by scraping bark and twigs from multiple areas of one tree and pooling the sample. The three spectra measured were similar with each having 11 main peaks with similar wavenumbers for each. Small differences in absorbance maxima are due to environmental variables such as water in the sample, dust, and plant contamination (Wadsten and Moberg 1985). The wavenumber for identifying the presence of calcium oxalate monohydrate was 1315 cm^{-1} (Figure 13, 14, 15). This absorption maximum is close to the pure whewellite absorption maximum of 1316 cm^{-1} (Garty et al. 2002). There are no peaks for calcium oxalate dihydrate (weddelite), which would have been found at 1326 cm^{-1} . All three spectra show two main peaks in the range between 590 and 690 cm^{-1} , which correspond to the spectral fingerprint of gypsum (Palacio et al. 2014). There is also a major peak at 1615 cm^{-1} which can be identified as the calcium oxalate C-O stretch (Palacio et al. 2014). Because the samples were collected in April 2019, there was abundant moisture present, and the peaks above 3000 cm^{-1} are due to O-H bonds in the water and cellulose molecules (Palacio et al. 2014).

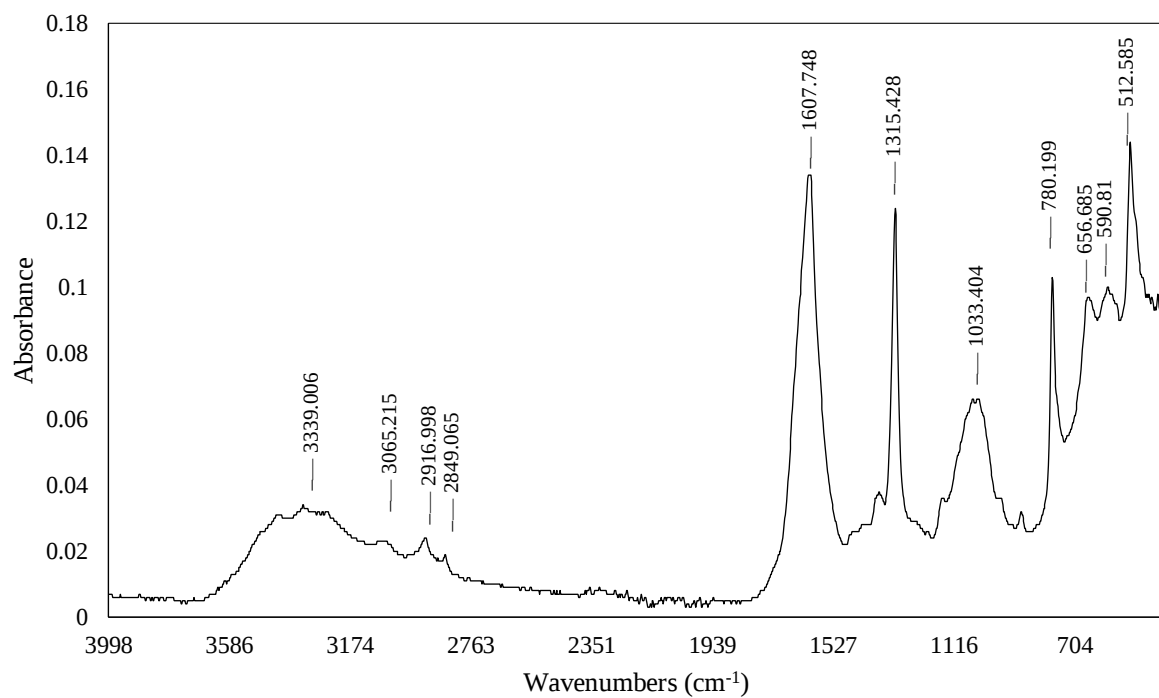


Figure 13. Infrared absorbance spectrum of white powder scraped from sample 1 bark and twig surfaces. Note the peak maxima at 1315 cm⁻¹ and 1606 cm⁻¹ indicating the presence of calcium oxalate monohydrate (CaC₂O₄ • H₂O).

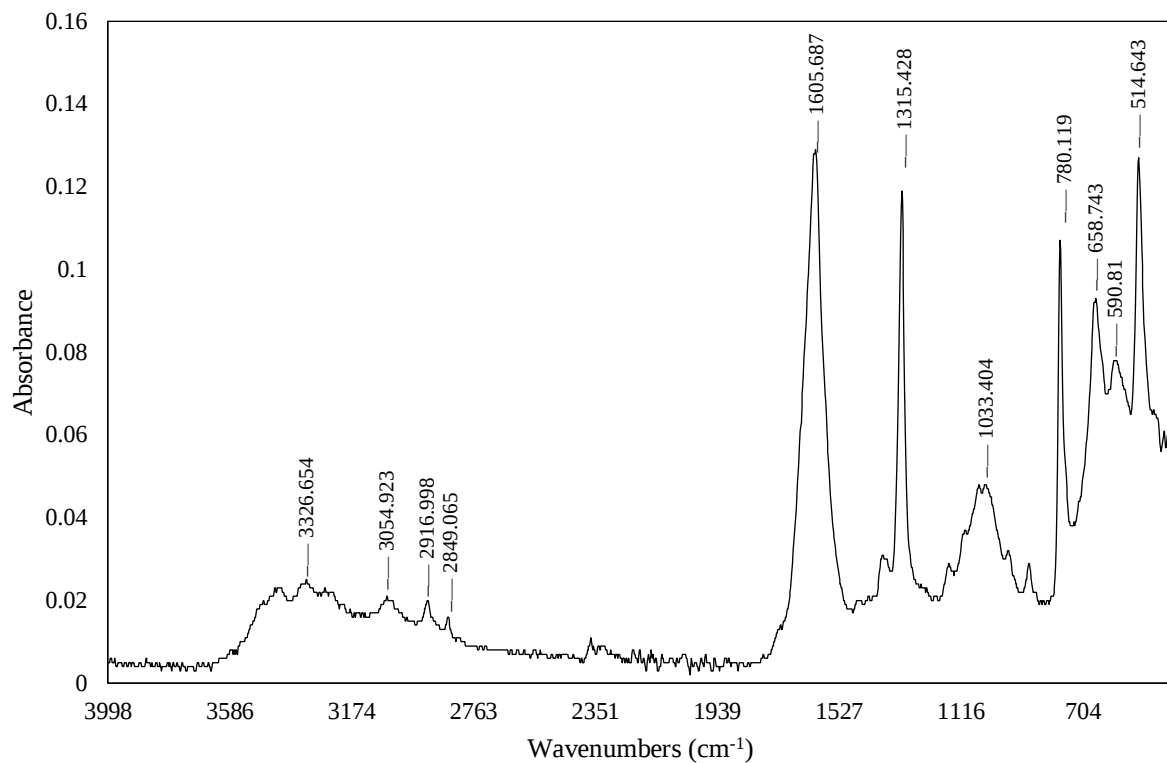


Figure 14. Infrared absorbance spectrum of white powder scraped from sample 2 bark and twig surfaces. Note the peak maxima at 1315 cm⁻¹ and 1605 cm⁻¹ indicating the presence of calcium oxalate monohydrate (CaC₂O₄ • H₂O).

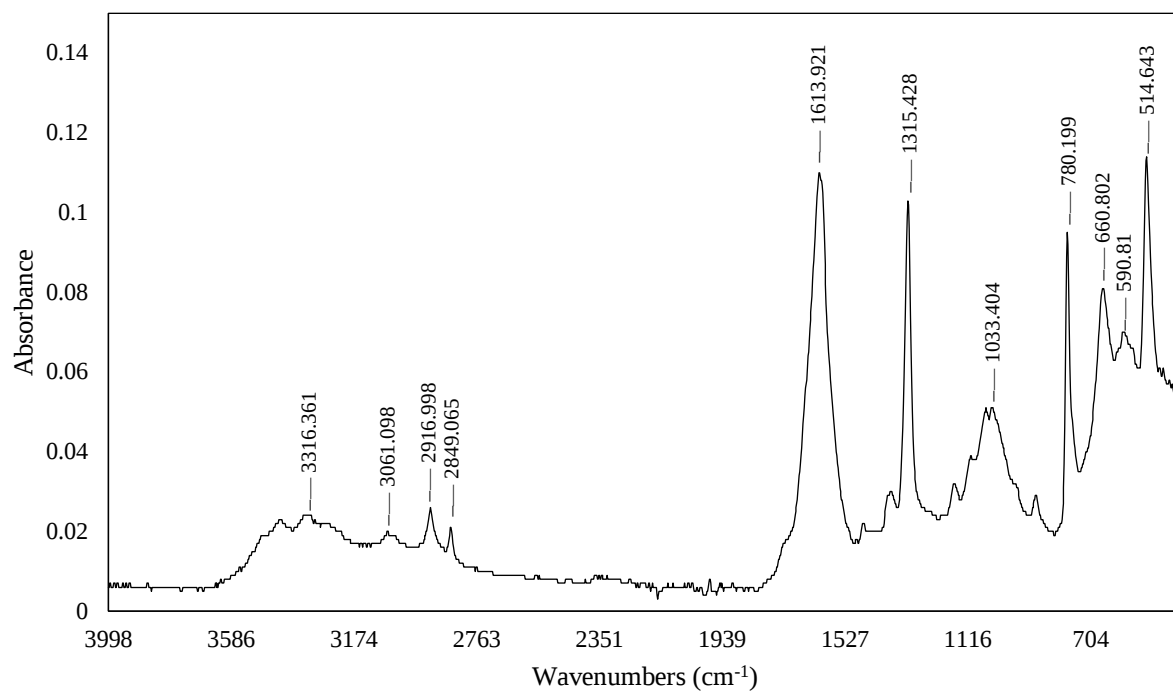


Figure 15. Infrared absorbance spectrum of white powder scraped from sample 3 bark and twig surfaces. Note the peak maxima at 1315 cm⁻¹ and 1613 cm⁻¹ indicating the presence of calcium oxalate monohydrate (CaC₂O₄ • H₂O).

Isolation of Pure Fungal Cultures

At the end of two months, 28 of the 45 plates (62%) showed growth of one or more fungal colonies. When the perithecia were dissected, 93% of the plates had fungal growth, which resulted in 37 pure cultures for DNA extraction. When the perithecia were ground in sterile water and then streaked on the plate, 53% of the plates had fungal growth, which resulted in 23 pure cultures for DNA extraction. When the perithecia could disperse their spores naturally, 33% of the plates had fungal growth, which resulted in 7 pure cultures for DNA extraction. When comparing medium type, of the initial cultures that had growth, 25% were grown on pure MEA, 15% on MEA + bark extract, 20% on pure bark extract, 15% on 50% bark extract, and 25% on 10% bark extract.

DNA from the resulting 67 pure cultures was amplified using PCR and resulted in successful amplification for 47 of the pure cultures along the 18S SSU region. The DNA of 59 pure cultures was amplified across the ITS 1 and 2 region (including 5.8S). Sanger sequencing, alignment, and clean up resulted in consensus sequences for 50 of the 67 pure cultures, 33 individuals along the SSU, and 49 individuals along the ITS region, 31 individuals resulted in successful sequences at both regions. Of all the sequences generated, 66% resulted from dissecting the ascocarp, 20% from grinding the ascocarp, and 14% from natural spore release. In terms of media, 56% of the fungi that were successful sequenced were grown on MEA medium and 44% on variations of the bark extract medium.

The ITS region is the universal fungal barcode for identifying fungi to species, however, due to the quality of the sequences and the high percent similarity in GenBank with many of the samples, identifications were done to genus and sometimes to order

when ITS data was not available. Sample diversity was broad and represented two major phyla, Ascomycota (96%) and Basidiomycota (4%). Ten main orders were represented (Figure 16) with 40% belonging to Pleosporales, 16% to Capnodiales, 16% to Botryosphaeriales, 2% to Chaetothyriales, 2% to Ostropales, 2% to Hypocreales, 12% to Xylariales, 2% to Agaricostibales, and 2% to Polyporales, with 6% that could not be identified down to order but were identified as belonging to class Dothideomycetes. Table 5 shows the species identified; cultures that were sequenced at both the 18S and ITS regions are represented as different sample numbers. Figure 17 shows the percent abundance of the classes of fungi identified, with Dothideomycetes being the most common at 78%. The percent abundance of each genera and the associated taxonomic classification are presented in Table 6. *Microdiplodia* was the most common fungus isolated, along with other common environmental contaminants such as *Cladosporium* and *Alternaria*

Robergea albicedrae was grown successfully in pure culture using 100% bark extract as the medium and natural spore dispersal as the means of inoculating the medium. The resultant growth was two small white colonies about 2–3 mm diameter. Only one of these colonies could be grown in pure culture and sequenced (sample ID: JRB_BC98) and resulted in a sequence (566 bp) spanning the ITS region. When searched against the GenBank database, the sequence aligned with the highest query cover and pairwise identity with taxa within the family Stictidaceae. It had the highest query coverage with *Robergea cubicularis* KY611899 (85.16%), with a pairwise identity of 83.9%.

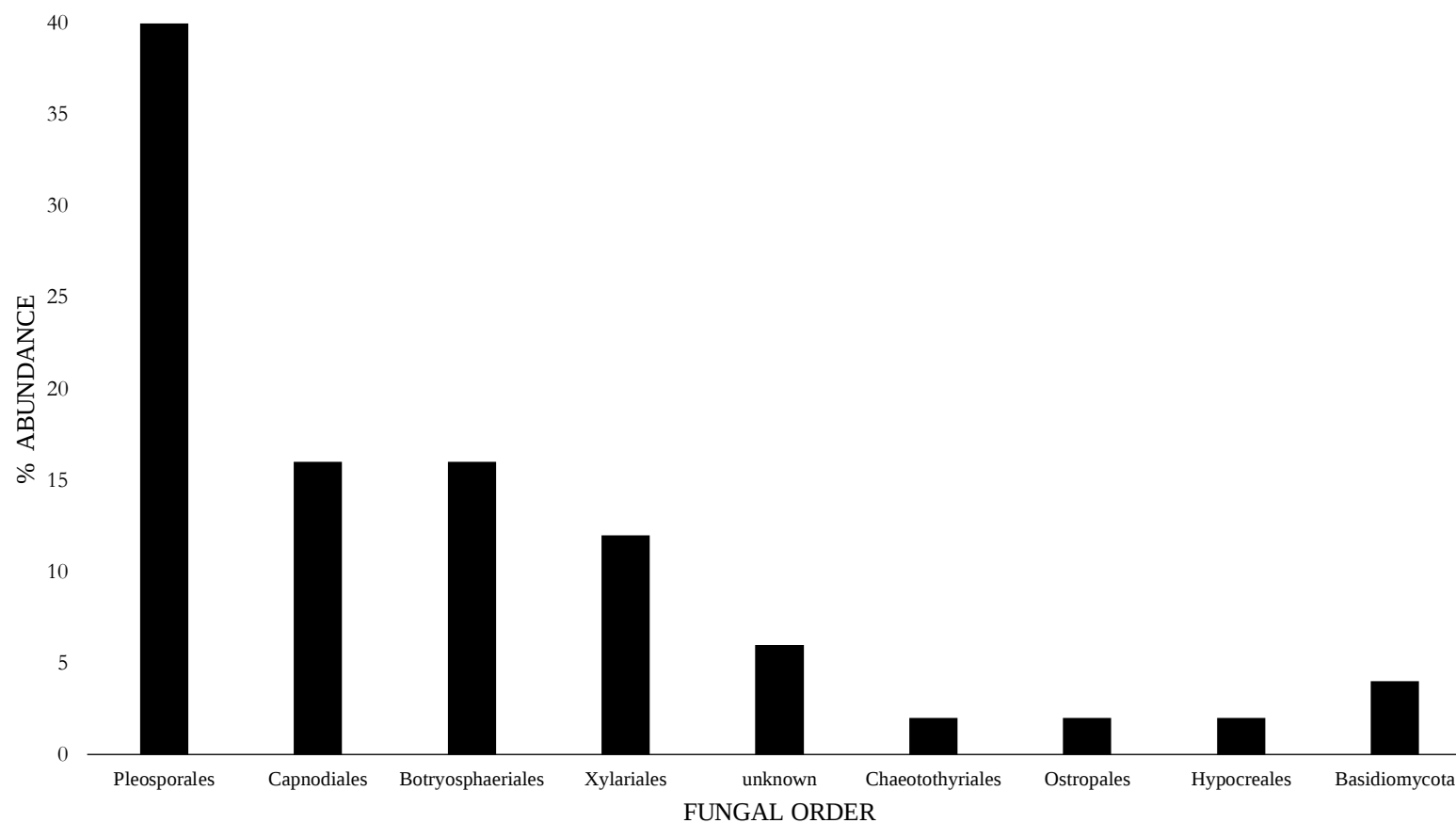


Figure 16. Percent abundance of fungal orders based on BLAST sequence data from the 50 pure cultures. Ten possible different orders were identified, with Pleosporales being the most common. Eight of the orders are placed within the phylum Ascomycota; Basidiomycota was represented by the orders Agaricostibales and Polyporales.

Table 5. Samples sequenced from bark pure cultures. Sample ID matches identifier in FASTA file (Appendix A). Samples identified based on reference organisms found using the NCBI GenBank database. Samples that were not bi-directionally checked have sequence read direction listed (forward or reverse).

Sample ID	Primers Used	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB_BC1	NS3/NS6	<i>Dothideomycetes</i> sp.	<i>Dothideomycetes</i> sp. GU324011	100	99.7	F
JRB_BC2	NS3/NS6	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. MH047202	99.89	100	X
JRB_BC5	NS3/NS6	Chionosphaeriaceae	<i>Kurtzmanomyces insolitus</i> KJ708424	100	93.7	X
JRB_BC7	NS3/NS6	Nectreaceae	<i>Xenoacremonium recifei</i> MK123331.1	100	100	R
JRB_BC9	NS3/NS6	<i>Alternaria</i> sp.	<i>Alternaria</i> sp. KT192438	100	99.9	X
JRB_BC13	NS3/NS6	Didymosphaeriaceae	<i>Didymosphaeria</i> NG_064914	98	100	R
JRB_BC14	NS3/NS6	Didymosphaeriaceae	<i>Didymosphaeria</i> NG_064914	100	100	X
JRB_BC16	NS3/NS6	Hypocreales	<i>Ustilaginoidea virens</i> MH780738	100	100	F
JRB_BC17	NS3/NS6	<i>Alternaria</i> sp.	<i>Alternaria</i> sp. MF184928	100	100	X
JRB_BC18	NS3/NS6	Phaeosphaeriaceae	<i>Septoria nodorum</i> U04236	100	100	X
JRB_BC19	NS3/NS6	Pleosporales	<i>Didymosphaeria variabile</i> NG_064914	100	99.86	F
JRB_BC20	NS3/NS6	Pleosporales	<i>Cucurbitodthis pityophila</i> U42480	100	100	X
JRB_BC23	NS3/NS6	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. MH047202	100	100	X
JRB_BC24	NS3/NS6	<i>Alternaria</i> sp.	<i>Alternaria</i> sp. MF184928	100	99.9	X

Table 5. Continued

Sample ID	Primers Used	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB_BC25	NS3/NS6	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. LT860211	100	99.44	F
JRB_BC27	NS3/NS6	Pleosporales	<i>Cucurbitodthis pityophila</i> U42480	100	100	X
JRB_BC28	NS3/NS6	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. isolate MN396375	100	98.89	R
JRB_BC29	NS3/NS6	Pleosporales	<i>Cucurbitodthis pityophila</i> U42480	100	100	X
JRB_BC30	NS3/NS6	Pleosporales	<i>Cucurbitodthis pityophila</i> U42480	100	100	X
JRB_BC31	NS3/NS6	Pleosporales	<i>Cucurbitodthis pityophila</i> U42480	100	100	X
JRB_BC32	NS3/NS6	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis</i> sp. AF346561	100	100	X
JRB_BC33	NS3/NS6	Pleosporales	<i>Cucurbitodthis pityophila</i> U42480	100	100	X
JRB_BC34	NS3/NS6	<i>Leptosphaerulina</i> sp.	<i>Leptosphaerulina</i> sp. KJ867215	100	100	X
JRB_BC35	NS3/NS6	Xylariales	<i>Pestalotiopsis guepinii</i> EU375526	100	100	X
JRB_BC36	NS3/NS6	Pleosporales	<i>Didymosphaeria variabile</i> NG_064914	100	100	F
JRB_BC37	NS3/NS6	<i>Alternaria</i> sp.	<i>Alternaria</i> sp. MF184928	100	100	X
JRB_BC39	NS3/NS6	Pleosporales	<i>Cucurbitodthis pityophila</i> U42480	100	100	X
JRB_BC41	NS3/NS6	<i>Rhizodiscina lignyota</i>	<i>Rhizodiscina lignyota</i> MF599193	100	98.3	X
JRB_BC43	NS3/NS6	Pleosporales	<i>Didymosphaeria variabile</i> ST NG_064914	100	99.71	F

Table 5. Continued

Sample ID	Primers Used	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB_BC44	NS3/NS6	Pleosporales	<i>Cucurbitodithis pityophila</i> U42480	100	100	X
JRB_BC45	NS3/NS6	Xylariales	<i>Pestalotiopsis</i> sp. KF776947	100	99.18	F
JRB_BC46	NS3/NS6	Didymellaceae	<i>Phoma</i> sp. AB252869	100	100	X
JRB_BC47	NS3/NS6	<i>Alternaria</i> sp.	<i>Alternaria</i> sp. MK855476	100	100	F
JRB_BC49	ITS1/ITS4	<i>Phaeococcomyces</i> sp.	<i>Phaeococcomyces</i> sp. MH474070	97	83.26	R
JRB_BC50	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium oxysporum</i> DQ912837	100	100	X
JRB_BC51	ITS1/ITS4	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis vismiae</i> AB251916	100	98.7	X
JRB_BC52	ITS1/ITS4	<i>Dothideomycetes</i> sp.	<i>Homortomyces tamaricis</i> KU934190	67.35	84.4	X
JRB_BC54	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. MN275887	100	96.97	R
JRB_BC55	ITS1/ITS4	Chionosphareaceae	<i>Ballistosporomyces sasicola</i> KY101699	60.41	79.7	X
JRB_BC56	ITS1/ITS4	<i>Paraconiothyrium</i> sp.	<i>Paraconiothyrium brasiliense</i> MK247586	100	99.78	R
JRB_BC57	ITS1/ITS4	<i>Fusarium</i> sp.	<i>Fusarium lateritium</i> FJ549977	100	99.75	R
JRB_BC58	ITS1/ITS4	<i>Epicoccum</i> sp.	<i>Epicoccum nigrum</i> KU204774	99.82	97.6	X
JRB_BC59	ITS1/ITS4	<i>Alternaria</i> sp.	<i>Alternaria alternata</i> MH221088	100	98.3	X

Table 5. Continued

Sample ID	Primers Used	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB_BC61	ITS1/ITS4	<i>Paraconiothyrium</i> sp.	<i>Paraconiothyrium brasiliense</i> MN429231	100	97.12	R
JRB_BC62	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium cladosporioides</i> KJ767066	99.82	95.9	X
JRB_BC65	ITS1/ITS4	<i>Paraconiothyrium</i> sp.	<i>Paraconiothyrium brasiliense</i> MK247586	100	99.78	R
JRB_BC66	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KF010841	99.84	95.1	X
JRB_BC67	ITS1/ITS4	Didymosphaeriaceae	<i>Paraconiothyrium brasiliense</i> MN429231.1	92	92.68	R
JRB_BC69	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. KM051396	100	99.8	X
JRB_BC70	ITS1/ITS4	<i>Alternaria</i> sp.	<i>Alternaria</i> sp. KR028000	100	100	X
JRB_BC72	ITS1/ITS4	<i>Phaeosphaeriopsis</i> sp.	<i>Phaeosphaeriopsis</i> sp. KX 788207	100	94	X
JRB_BC73	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KY421921	100	98.7	X
JRB_BC74	ITS1/ITS4	<i>Paraconiothyrium</i> sp.	<i>Paraconiothyrium fuckelii</i> KJ939278	100	94.8	X
JRB_BC75	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KY421921	100	98.9	X
JRB_BC76	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium oxysporum</i> MH844757	100	100	X
JRB_BC77	ITS1/ITS4	Lophiotremataceae	<i>Atrocalyx bambusae</i> NR_153559	100	93.92	R

Table 5. Continued

Sample ID	Primers Used	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB_BC78	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. MH047202	100	99.6	X
JRB_BC79	ITS1/ITS4	<i>Alternaria</i> sp.	<i>Alternaria alternata</i> KU179665	100	100	X
JRB_BC80	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. MN128233	100	96.8	X
JRB_BC81	ITS1/ITS4	Pleosporineae	<i>Coniothyrium pyrinum</i> MK907750	99	97.35	R
JRB_BC82	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KY421921	99.67	98.5	X
JRB_BC83	ITS1/ITS4	<i>Cladosporium</i> sp.	<i>Cladosporium</i> sp. MH047202	95.38	92.6	X
JRB_BC84	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KY421921	100	98.7	X
JRB_BC85	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KY421921	100	95.1	X
JRB_BC86	ITS1/ITS4	<i>Paraconiothyrium</i> sp.	<i>Paraconiothyrium</i> <i>brasiliense</i> LT796895	100	97.6	X
JRB_BC87	ITS1/ITS4	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis microspore</i> KY366172	100	97.2	X
JRB_BC89	ITS1/ITS4	<i>Pithomyces</i> sp.	<i>Pithomyces chartarum</i> MH860299	100	97.2	X
JRB_BC90	ITS1/ITS4	<i>Daldinia</i> sp.	<i>Daldinia eschscholtzii</i> MN192994	100	97.9	R
JRB_BC91	ITS1/ITS4	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis microspore</i> KY366172	100	97.7	X
JRB_BC92	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KF010841	100	99.2	X

Table 5. Continued

Sample ID	Primers Used	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB_BC93	ITS1/ITS4	<i>Alternaria</i> sp.	<i>Alternaria tenuissima</i> MH999495	100	99.7	X
JRB_BC95	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KF010841	100	98.5	X
JRB_BC96	ITS1/ITS4	<i>Microdiplodia</i> sp.	<i>Microdiplodia</i> sp. KY421921	100	94.8	X
JRB_BC97	ITS1/ITS4	<i>Dothideomycetes</i> sp.	<i>Dothideomycetes</i> sp. AB986429	100	83.4	X
JRB_BC98	ITS1/ITS4	<i>Robergea</i> sp.	<i>Robergea cubicularis</i> KY611899	85.16	83.9	R
JRB_BC99	ITS1/ITS4	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis neglecta</i> DQ000992	100	98.4	X
JRB_BC101	ITS1/ITS4	<i>Paraconiothyrium</i> sp.	<i>Paraconiothyrium brasiliense</i> LT796895	100	98.7	R
JRB_BC102	ITS1/ITS4	<i>Trametes</i> sp.	<i>Trametes cubensis</i> MN068933	100	98.2	R
JRB_BC103	ITS1/ITS4	<i>Paraconiothyrium</i> sp.	<i>Paraconiothyrium brasiliense</i> MK247586	99.82	99.8	R
JRB_BC104	ITS1/ITS4	<i>Pestalotiopsis</i> sp.	<i>Pestalotiopsis neglecta</i> DQ000992	100	98.4	X
JRB_BC105	ITS1/ITS4	<i>Epicoccum</i> sp.	<i>Epicoccum</i> sp. KT192409	100	99.1	R
JRB_BC107	ITS1/ITS4	<i>Alternaria</i> sp.	<i>Alternaria tenuissima</i> MH999495	100	99.7	X

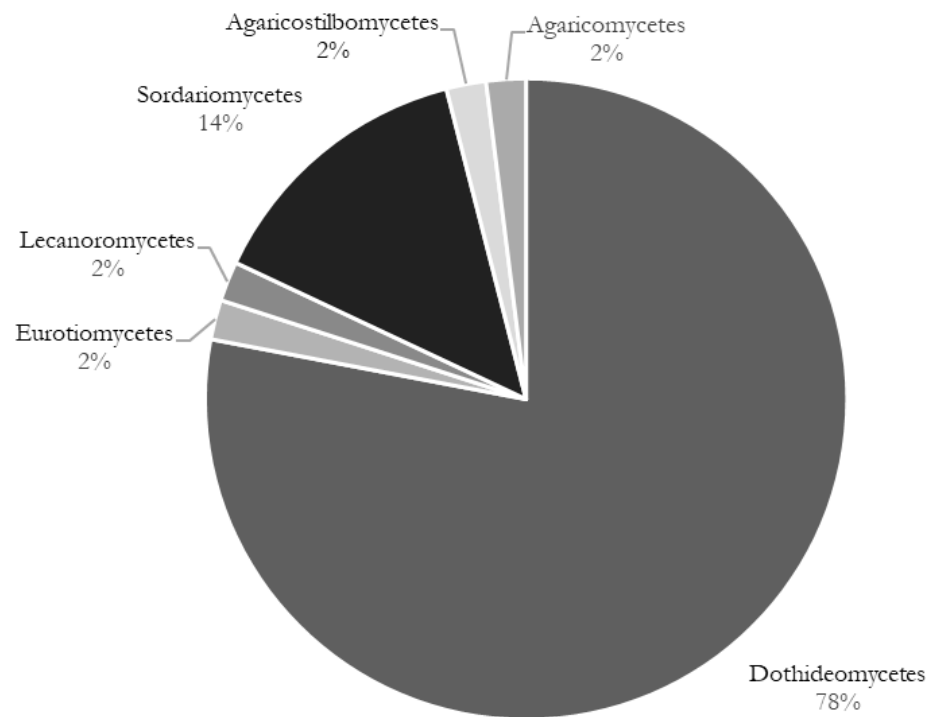


Figure 17. Percent abundance of each fungal class based on BLAST sequence data from the 50 pure cultures. Six different classes identified, with Dothideomycetes being the most common. Four of the classes are placed within the Phylum Ascomycota; Basidiomycota was represented by the classes Agaricostilbomycetes and Agaricomycetes.

Table 6. Fungal diversity based on DNA sequences from pure cultures. Most sequences were supported by regions of the 18S SSU nuDNA and ITS. Two phyla are represented (Ascomycota and Basidiomycota), along with as many as 10 different genera. Most of the genera represented are common plant pathogens and can occur in a wide variety of habitats, most notably woody plant tissue. *unknown

Genus	Family	Order	Class	Division	% abundance by fungal genera
*	*	*	Dothideomycetes	Ascomycota	6
*	*	Pleosporales	Dothideomycetes	Ascomycota	2
*	Lophiotremataceae	Pleosporales	Dothideomycetes	Ascomycota	2
*	Phaeosphaeriaceae	Pleosporales	Dothideomycetes	Ascomycota	2
<i>Alternaria</i>	Pleosporaceae	Pleosporales	Dothideomycetes	Ascomycota	10
<i>Cladosporium</i>	Cladsporiaceae	Capnodiales	Dothideomycetes	Ascomycota	16
<i>Epicoccum</i>	Pleosporaceae	Pleosporales	Dothideomycetes	Ascomycota	2
<i>Leptosphaerulina</i>	Astrosphaeriellaceae	Pleosporales	Dothideomycetes	Ascomycota	2
<i>Microdiplodia</i>	Botryosphaeriaceae	Botryosphaeriales	Dothideomycetes	Ascomycota	16
<i>Paraconiothyrium</i>	Didymosphariaceae	Pleosporales	Dothideomycetes	Ascomycota	20
<i>Phaeococcomyces</i>	Herpotrichiellaceae	Chaetothyriales	Eurotiomycetes	Ascomycota	2
<i>Robergea</i>	Stictidaceae	Ostropales	Lecanoromycetes	Ascomycota	2
<i>Daldinia</i>	Hypoxylaceae	Xylariales	Sordariomycetes	Ascomycota	2
<i>Fusarium</i>	Nectriaceae	Hypocreales	Sordariomycetes	Ascomycota	2
<i>Pestalotiopsis</i>	Sporocadaceae	Xylariales	Sordariomycetes	Ascomycota	10
<i>Trametes</i>	Polyporaceae	Polyporales	Agaricomycetes	Basidiomycota	2
*	Chionosphaeraceae	Agaricostibales	Agaricostilbomycetes	Basidiomycota	2

Molecular Assessment

Primary DNA extractions of the excised perithecia from *Robergea albicedrae* using the Gentra PureGene DNA Extraction Kit (Qiagen) were not successful, except in the case of the pure cultures from the bark mycoflora experiment. Subsequent extractions using the amended CTAB protocol listed before were successful, yielding a good DNA pellet, however upon rehydration, the DNA was highly pigmented (possibly from secondary plant compounds). This interfered with PCR amplification and variations of multiple dilutions were used depending on the PCR results. For most of the successful PCR amplification reactions 5.0 µL of 1:100 diluted template DNA was used. The internal transcribed spacer region was successfully sequenced twice (542 bp and 567 bp) using Sanger deoxy sequencing early in the research, however sequencing of the SSU and LSU regions was not successful (short sequences, low base quality, or missing forward or reverse sequence). When these two ITS sequences were compared to the NCBI database using a BLAST search, they showed 74% and 71% similarity to *Robergea cubicularis*, is the only other taxon in the genus with molecular data present in GENBANK. The list of the top 30 hits for both sequences contained only members of the order Ostropales, with most falling within the family Stictidaceae.

Due to the limited quality of these ITS sequences and in an attempt to sequence the SSU, the original samples were cloned using the TOPO TA cloning kit. Two subsequent cloning experiments were conducted using the original template DNA. Two regions on the 18S SSU (Table 1) and the ITS region were cloned. The first cloning did not result in any successful DNA sequences, while the second cloning experiment resulted in ten sequences for the SSU, two using primer set NS3/NS6 and eight using

primer set nssu131/NS4. None of these sequences showed BLAST search results positive for *Robergea albicedrae*, but they did have positive identifications for other common fungal endophytes and the NS3/NS6 resulted in one plant taxon being identified (*Monarda fistulosa*). Repeated efforts to get sequences for the SSU and cleaner sequences for the ITS region were hampered as PCR conditions were not successful in amplifying the DNA, the product that was yielded produced very few clones, and the few clones that were grown failed to be sequenced successfully. Adjustments in PCR master mix reagents such as +/- magnesium chloride, +/- BSA, using different primers (LROR/LR7 and RPB1AFasc/RPB16R1asc), and adjustments in thermocycling conditions all failed to result in successful sequencing of *R. albicedrae*.

The focus was narrowed in order to get successful sequences using primers nssu131 and NS4. Due to the low melting temperature for these primers, the annealing temperature was lowered to 45°C and the resulting PCR reactions were successful. The original samples, along with the 16 environmental samples, were amplified using this protocol and the resultant 15 samples were cloned. Out of the 15 samples, 14 plates had successful bacterial growth. Eight colonies from each plate were chosen and these samples were amplified using the kit supplied primers (T3/T7), resulting in 45 successful products to be sequenced. These sequences yielded a wide and diverse variety of fungal endophytes, with two sequences identifying the green alga *Trebouxia* sp., and one successful sequence for *R. albicedrae* for the SSU (Table 6). Despite numerous attempts, the tDNA could not be cloned for the ITS region. Efforts to sequence the ITS region using next generation sequencing via the Earth Microbiome Project Illumina protocol (Thompson et al. 2017) were not successful.

Table 7. Identified taxa based on 18S SSU rDNA and ITS 1 and 2 sequence data collected from clones and environmental samples. The FASTA sequences are listed in Appendix A. Samples were identified based on reference organisms using the NCBI GenBank database. Samples that were not bi-directionally checked have sequence read direction listed (forward or reverse).

Sample ID	Primer	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRBT100_E11E12	ITS1/ITS4	Stictidaceae sp.	<i>Stictis urceolatum</i> HQ650601	40.18	92.8	X
JRBB100_G11G12	ITS1/ITS4	Stictidaceae sp.	<i>Stictis radiata</i> MH578502	41.73	88.3	R
JRBB100_H11H12	ITS1/ITS4	Stictidaceae sp.	<i>Stictis radiata</i> AY527308	73.43	88.3	X
JRBT100_A11A12	NS3/NS6	Pezizomycotina	<i>Coccotrema pocillarium</i> AF274113	45	100	X
JRB009_17_25	nssu131/NS4	Lecanoromycetes sp.	<i>Cladonia caroliniana</i> AY584664	91.18	86.4	X
JRB011_65_73	nssu131/NS4	Dothideomycetes sp.	Dothideomycetes sp. KF680803	100	97.1	X
JRB011_66_74	nssu131/NS4	Orbiliaceae sp.	<i>Monacrosporium</i> <i>gephyropagum</i> AJ001996	100	98.8	X
JRB011_68_76	nssu131/NS4	Orbiliaceae sp.	<i>Dactylella clavata</i> NM_062731	100	98.6	X
JRB011_69_77	nssu131/NS4	<i>Rhizana undulata</i>	<i>Rhizina undulata</i> U42664	100	96.5	X
JRB011_70_78	nssu131/NS4	Teratosphaeriaceae sp.	Teratosphaeriaceae sp. GU250356	100	96.6	R
JRB011_71_79	nssu131/NS4	<i>Rhinocladiella</i> sp.	<i>Rhinocladiella</i> sp. AJ972862	100	98.5	R
JRB011_72_80	nssu131/NS4	Phaeococcomycetaceae sp.	Phaeococcomycetaceae sp. GU324016	100	98.9	R
JRB015_81_89	ITS1/ITS4	<i>Exophiala</i> sp.	<i>Exophiala</i> sp. EU035420	85.91	91.7	X

Table 7. Continued

Sample ID	Primer	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB015_82_90	ITS1/ITS4	<i>Komagataella phaffii</i>	<i>Komagataella phaffii</i> CP014719	97.27	99.7	X
JRB015_83_91	ITS1/ITS4	<i>Aureobasidium</i> sp.	<i>Aureobasidium</i> sp. KY089087	100	81.5	X
JRB015_84_92	ITS1/ITS4	<i>Trebouxia</i> sp.	Uncultured <i>Trebouxia</i> AM159214	94.77	99.2	R
JRB015_85_93	ITS1/ITS4	<i>Trebouxia</i> sp.	Uncultured <i>Trebouxia</i> AM159214	100	99.2	R
JRB015_86_94	ITS1/ITS4	<i>Caloplaca</i> sp.	<i>Caloplaca camtidia</i> MK089355	99.68	95.3	X
JRB015_87_95	ITS1/ITS4	<i>Banhegyia</i> sp.	<i>Banhegyia setispora</i> KY654747	97.17	96.5	R
JRB015_88_96	ITS1/ITS4	<i>Trichomerium</i> sp.	<i>Trichomerium</i> sp. MH345731	97.99	95.6	X
JRB002_33_41	nssu131/NS4	<i>Rhizodiscina lignyota</i>	<i>Rhizodiscina lignyota</i> MF599193	99.89	96.2	X
JRB002_34_42	nssu131/NS4	<i>Knufia</i> sp.	<i>Knufia epidermidis</i> KP174872	100	98.9	R
JRB002_35_43	nssu131/NS4	<i>Coniosporium</i> sp.	<i>Coniosporium</i> sp. AJ972863	100	99.2	R
JRB002_36_44	nssu131/NS4	<i>Rhizodiscina lignyota</i>	<i>Rhizodiscina lignyota</i> MF599193	100	96.6	R
JRB002_37_45	nssu131/NS4	Capnodiales sp.	Capnodiales sp. KC315868	100	99.1	R
JRB002_38_46	nssu131/NS4	<i>Rhizodiscina lignyota</i>	<i>Rhizodiscina lignyota</i> MF599193	100	96.4	R
JRB002_39_47	nssu131/NS4	<i>Coniosporium</i> sp.	<i>Coniosporium</i> sp. AJ972863	100	97.8	R
JRB002_40_48	nssu131/NS4	<i>Coniosporium</i> sp.	<i>Coniosporium</i> sp. Y11712	99.74	98.6	F

Table 7. Continued

Sample ID	Primer	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB004_52_60	nssu131/NS4	<i>Astrosphaeriellopsis</i> sp.	<i>Astrosphaeriellopsis caryotae</i> NG_063600	75.74	98.9	X
JRB004_53_61	nssu131/NS4	<i>Deviesia compacta</i>	<i>Deviesia compacta</i> NG_064945	100	97.4	R
JRB004_54_62	nssu131/NS4	<i>Sarea resinae</i>	<i>Sarea resinae</i> AY641004	100	94.4	R
JRB004_55_63	nssu131/NS4	<i>Anguillospora rosea</i>	<i>Anguillospora rosea</i> AY357265	99.64	97.9	R
JRB004_56_64	nssu131/NS4	Capnodiales sp.	Capnodiales sp. GU323193	99.5	99.1	X
JRB_TB_CL10.18_108	nssu131/NS4	<i>Amycosphaerella keniensis</i>	<i>Amycosphaerella keniensis</i> NG_062384	100	96.9	X
JRB_TB_CL10.18_109	nssu131/NS4	<i>Orbilia</i> sp.	<i>Orbilia</i> sp. KY419196	99.64	97.7	R
JRB_TB_CL10.18_110	nssu131/NS4	<i>Slimacomyces isiola</i>	<i>Slimacomyces isiola</i> AB620069	99.89	98.3	X
JRB_TB_CL10.18_114	nssu131/NS4	Eurotiomycetes sp.	Eurotiomycetes sp. KP115824	100	98.8	X
JRB_TB_CL10.18_115	nssu131/NS4	Phaeococcomycetaceae sp.	Phaeococcomycetaceae sp. GU250330	92.41	99.0	X
JRB_TB_CL10.18_116	nssu131/NS4	Chaetothyriales sp.	Chaetothyriales sp. FJ358335	100	94.7	F
JRB_TB_CL10.18_117	nssu131/NS4	<i>Anguillospora rosea</i>	<i>Anguillospora rosea</i> AY357265	100	98.5	X
JRB_TB_CL10.18_118	nssu131/NS4	<i>Minutisphaera parafimbriatispora</i>	<i>Minutisphaera parafimbriatispora</i> KP310003	92.47	95	X
JRB_TB_CL10.18_119	NS3/NS6	<i>Monarda fistulosa</i>	<i>Monarda fistulosa</i> KT179704	93.21	99.6	F
JRB_TB_CL10.18_120	NS3/NS6	<i>Monarda fistulosa</i>	<i>Monarda fistulosa</i> KT179704	91.93	99.6	F

Table 7. Continued

Sample ID	Primer	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRBT100_CL09.19_05	nssu131/NS4	<i>Mycosphaerella euryptami</i>	<i>Mycosphaerella euryptami</i> GU47961	100	87.7	R
JRBT100_CL09.19_06	nssu131/NS4	Chaetothyriales sp.	Chaetothyriales sp. FJ358327	100	99.1	R
JRBT100_CL09.19_08	nssu131/NS4	<i>Tiarosporella dactylidis</i>	<i>Tiarosporella dactylidis</i> KM978947	21.25	98.6	R
JRBT100_CL09.19_11	nssu131/NS4	Stictidaceae sp.	<i>Stictis radiata</i> U20610	31.63	98	X
JRBT100_CL09.19_12	nssu131/NS4	Stictidaceae sp.	<i>Acarosporina microspora</i> AY584667	72.5	98.4	R
JRBT100_CL09.19_13	nssu131/NS4	<i>Phoma</i> sp.	<i>Phoma</i> sp. EF532930	98.66	99.5	X
JRB002_CL09.19_14	nssu131/NS4	<i>Chlorophyta</i> sp.	Uncultured <i>Chlorophyta</i> JQ627431	94.42	94	X
JRB002_CL09.19_15	nssu131/NS4	<i>Trebouxia</i> sp.	Uncultured <i>Trebouxia</i> JX169846	100	94.3	X
JRB002_CL09.19_16	nssu131/NS4	<i>Rhizodiscina lignyota</i>	<i>Rhizodiscina lignyota</i> MF599193	100	96.5	F
JRB002_CL09.19_17	nssu131/NS4	<i>Rhizodiscina lignyota</i>	<i>Rhizodiscina lignyota</i> MF599193	99.8	96.2	X
JRB002_CL09.19_18	nssu131/NS4	<i>Rhizodiscina lignyota</i>	<i>Rhizodiscina lignyota</i> MF599193	99.2	96	X
JRB002_CL09.19_19	nssu131/NS4	Chaetothyriales sp.	Chaetothyriales sp. KX822490	90/68	94.6	X
JRB002_CL09.19_20	nssu131/NS4	<i>Melanops</i> sp.	<i>Melanops</i> sp. FJ824763	100	98.1	X
JRB002_CL09.19_21	nssu131/NS4	Letiomycetes sp.	<i>Infundichalara microchona</i> NG_061112	100	96.4	X
JRB003_CL09.19_22	nssu131/NS4	<i>Guignardia</i> sp.	<i>Guignardia mangiferae</i> EU781482	99.59	97	X
JRB003_CL09.19_23	nssu131/NS4	<i>Arthrocladium caudatum</i>	<i>Arthrocladium caudatum</i> LT558701	90.80	98.6	X

Table 7. Continued

Sample ID	Primer	Organism ID	Reference Organism	Query Coverage (%)	Pairwise ID (%)	Bi-directionally checked
JRB003_CL09.19_24	nssu131/NS4	Phaeococcomycetaceae sp.	Phaeococcomycetaceae sp. GU324016	86.14	98	X
JRB003_CL09.19_25	nssu131/NS4	<i>Guignardia</i> sp.	<i>Guignardia philoprina</i> FJ824760	88.88	96.4	X
JRB003_CL09.19_26	nssu131/NS4	<i>Apatococcus</i> sp.	<i>Apatococcus</i> sp. KX025108	100	99.8	X
JRB003_CL09.19_28	nssu131/NS4	<i>Kellermania</i> sp.	<i>Kellermania confuse</i> NG_062176	100	96.2	X
JRB005_CL09.19_29	nssu131/NS4	<i>Anguillospora rosea</i>	<i>Anguillospora rosea</i> AY357265	97.54	97.6	X
JRB005_CL09.19_30	nssu131/NS4	Capnodiales sp.	Capnodiales sp. KC315868	100	98.7	X
JRB005_CL09.19_31	nssu131/NS4	<i>Cladosporium</i> sp.	<i>Cladosporium endophytica</i> NG_065726	100	98	X
JRB005_CL09.19_33	nssu131/NS4	<i>Coniosporium</i> sp.	<i>Coniosporium</i> sp. AJ972863	100	98.3	X
JRB010_CL09.19_34	nssu131/NS4	<i>Veronaea botryose</i>	<i>Veronaea botryose</i> NG_061120	97.91	98.3	X
JRB010_CL09.19_35	nssu131/NS4	<i>Bulgariella pulla</i>	<i>Bulgariella pulla</i> KU845534	92.58	94.1	X
JRB010_CL09.19_36	nssu131/NS4	<i>Polycephalomyces nipponicus</i>	<i>Polycephalomyces nipponicus</i> MG725823	91.41	96.5	X
JRB010_CL09.19_37	nssu131/NS4	<i>Rhinocladiella</i> sp.	<i>Rhinocladiella</i> sp. AJ972862	83.30	96.4	X
JRB010_CL09.19_38	nssu131/NS4	<i>Clathrospora diplospora</i>	<i>Clathrospora diplospora</i> U43464	57.75	98.3	X
JRB010_CL09.19_39	nssu131/NS4	<i>Bullera unica</i>	<i>Bullera unica</i> NG_063531	91.95	93.6	X
JRB011_CL09.19_41	nssu131/NS4	<i>Sirobasidium</i> sp.	<i>Sirobasidium japonicum</i> LC203424	99.75	98.7	X
JRB012_CL09.19_43	nssu131/NS4	<i>Melanops</i> sp.	<i>Melanops</i> sp. FJ824763	92.17	98.4	X

Phylogenetics

Sequence data was chosen for both the 18S SSU and ITS 1 and 2 regions based on the percent identity and query cover when compared with the *R. albicedrae* sequences in GenBank. Sequence data was limited within the genus *Robergea*, so accession lists to include as many similar species as possible were compiled. The data matrix was analyzed using neighbor joining distance methods with a GTR + I + g substitution model. The neighbor joining tree comparing the 18S region (Figure 18) resulted in a bootstrap consensus tree with a polytomy between most of the families compared. There was strong support for the family Wiesneriomycetaceae (100%). In general, there was good support for clades between species of the same family, all the Sclerococcaceae and Teloschistaceae were grouped, and all the species in Stictidaceae were grouped within two main clades except for *Cyanodermella viridula*. One *Robergea* sample (JRBT100_CL0919_11) was nested within the order Ostropales and among the other members of Stictidaceae. The phylogeny inferred from Bayesian analysis (Figure 19) confirmed the neighbor joining tree, but with even better support for the *Cryptodiscus* clade, the order Teloschistales, and the family Stictidaceae. *Robergea* was nested with *Conotrema*, *Stictis*, and *Acarosporina* with 89% confidence. The divergence of the early nodes in this phylogeny was not supported, creating a polytomy between the families. Stictidaceae was divided into two main clades, but support for each clade was above 0.89.

Figure 20 shows the comparison of 351 bp of the ITS 1 and 2 region. This is a highly variable region that does not get translated and spans the region between the SSU and LSU genes. The neighbor joining and Bayesian phylogenies compared two main

orders, Ostropales and Helotiales, as shown in Figure 21. The neighbor joining tree showed a strong and clear divergence between Helotiales and Ostropales. Within the Ostropalean clade, there was strong support for the genera *Phacidiella*, *Schizoxylon*, and *Stictis* (Figure 21). There was 100% consensus support for the grouping of the two *Robergea albicedrae* samples.

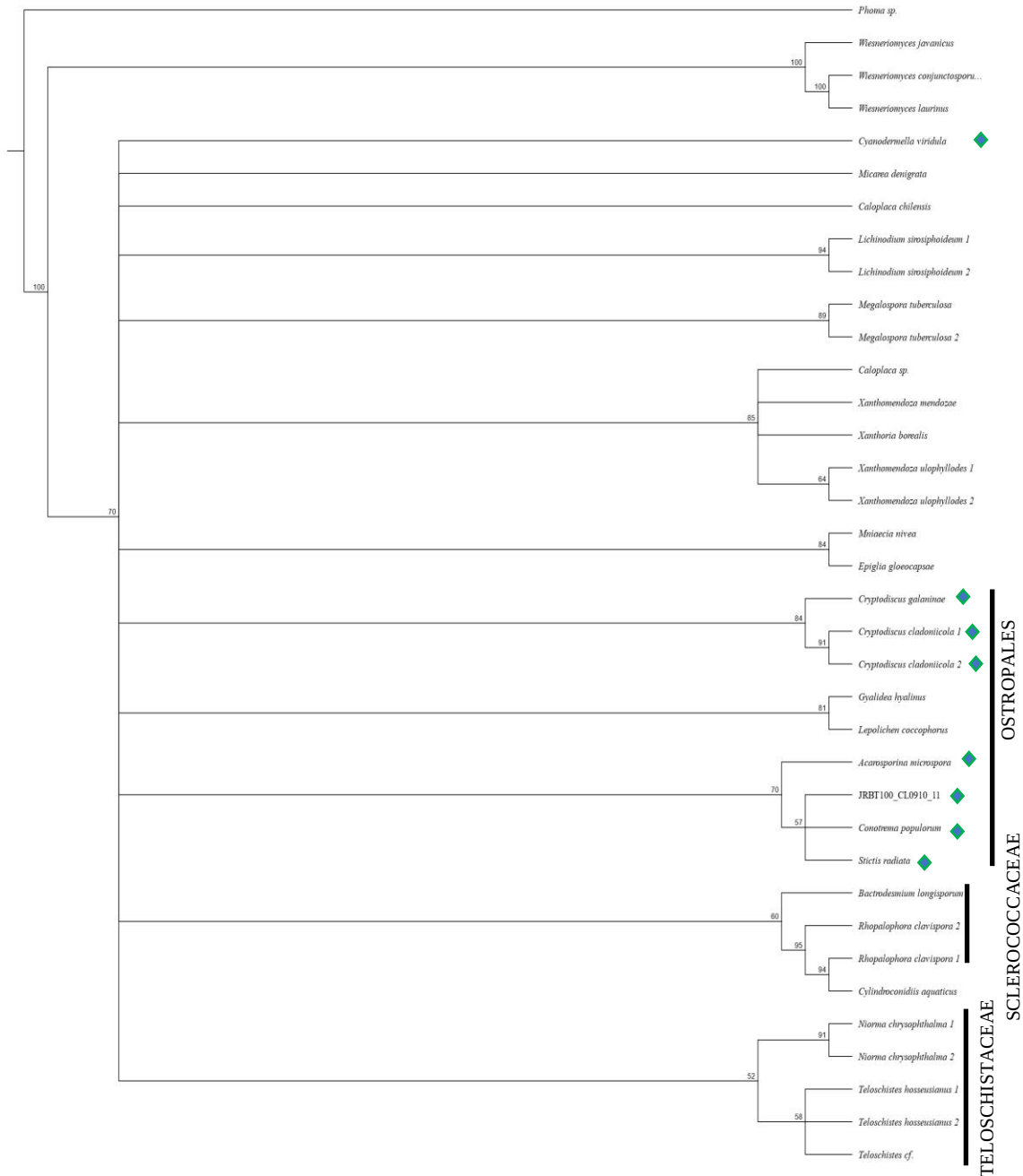


Figure 18. Phylogenetic relationships comparing 269 bp 18 S SSU rDNA molecular data for 36 ascomycetes including *Robergea albicedrae* sample, JRBT100_CL0910_11. This tree was generated using neighbor joining distance method with general time reversible substitution model with gamma distribution using Geneious 2019.2.1. *Phoma* sp. was set as the outgroup and rooted so the outgroup would be a monophyletic sister group to the ingroup. Bootstrap consensus tree from 1000 replications, bootstrap consensus support values presented on each branch. Green diamond = Members of Stictidaceae.

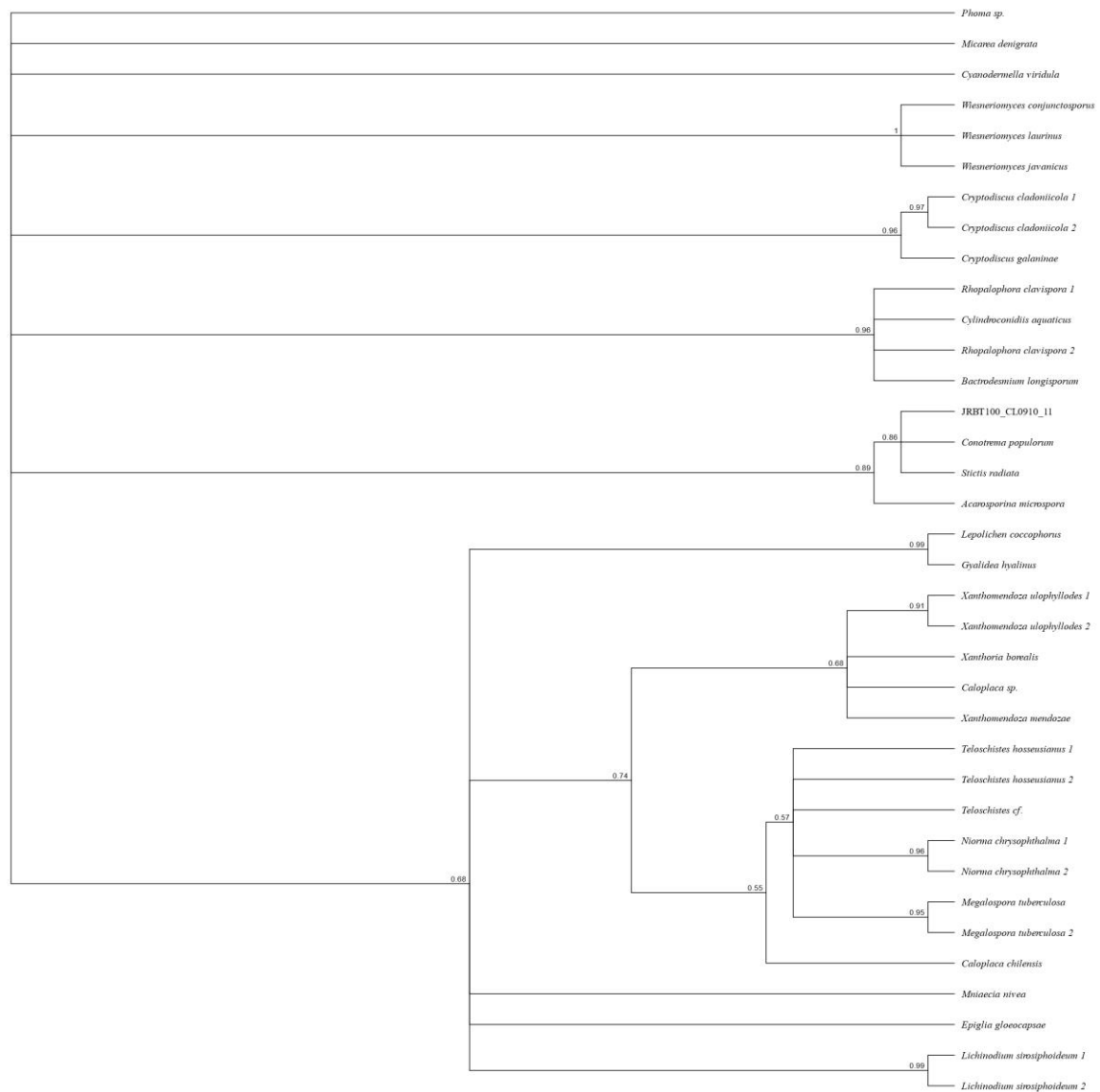


Figure 19. Phylogenetic relationships comparing 269 bp 18S SSU rDNA molecular data for 36 ascomycetes including *Robergea albicedrae* sample, JRBT100_CL0910_11. This tree was generated from 50% majority rule consensus of 2,500,000 trees analyzed with MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) Bayesian analysis using Markov chain Monte Carlo sampling within Geneious 2019.2.1. *Phoma* sp. was set as the outgroup and rooted so the outgroup would be a monophyletic sister group to the ingroup. Posterior probabilities presented above each branch, MCMC chain length = 1,100,000, subsample frequency = 200, and heated chains = 4.

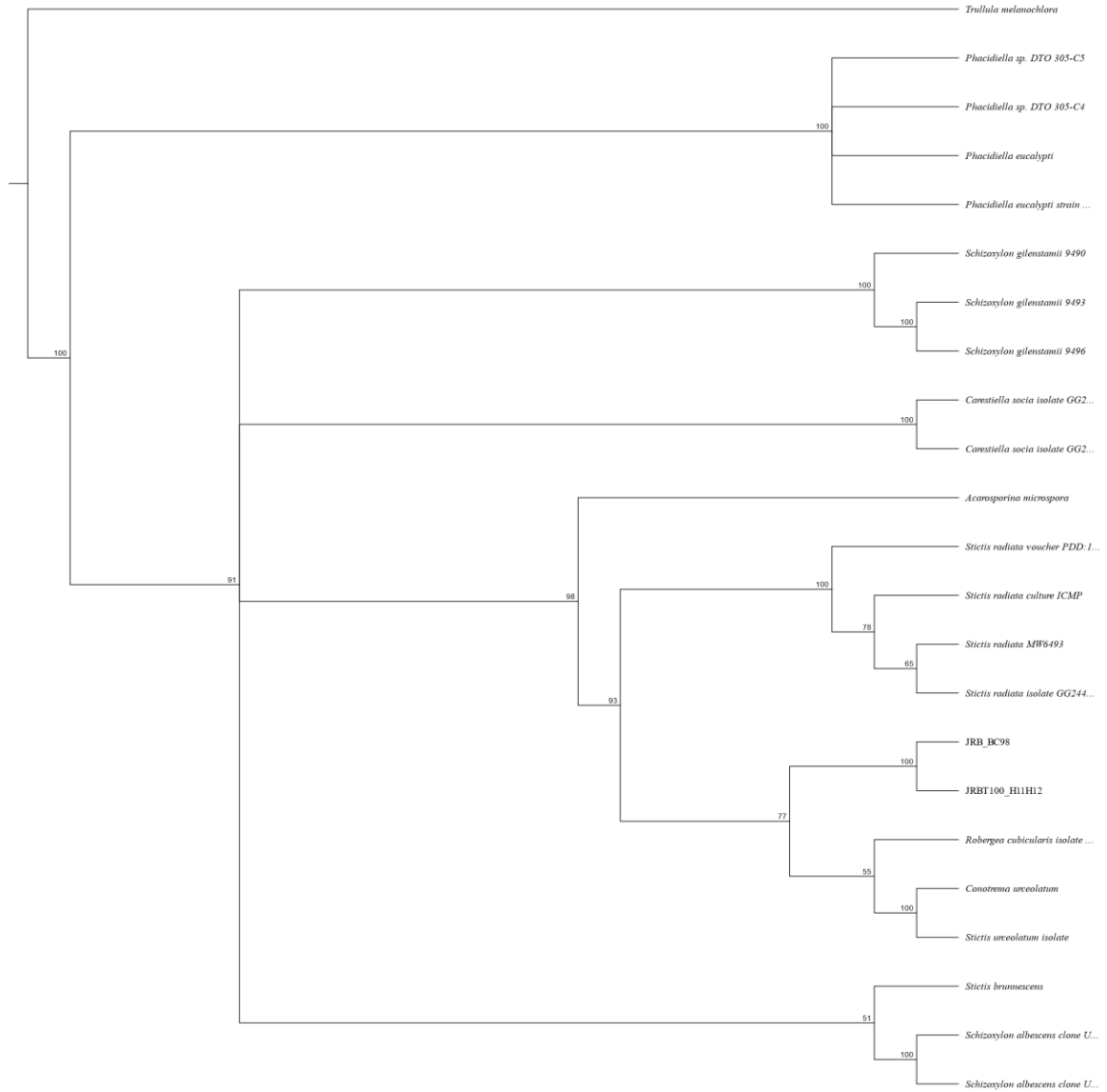


Figure 20. Phylogenetic relationships comparing 351 bp ITS rDNA molecular data for 23 ascomycetes including *Robergea albicedrae* samples, JRB_BC98 and JRBT100_H11H12. This tree was generated using neighbor joining distance method with general time reversible substitution model with gamma distribution using Geneious 2019.2.1. *Phoma* sp. was set as the outgroup and rooted so the outgroup would be a monophyletic sister group to the ingroup. Bootstrap consensus tree from 1000 replications, bootstrap consensus support values presented on each branch.

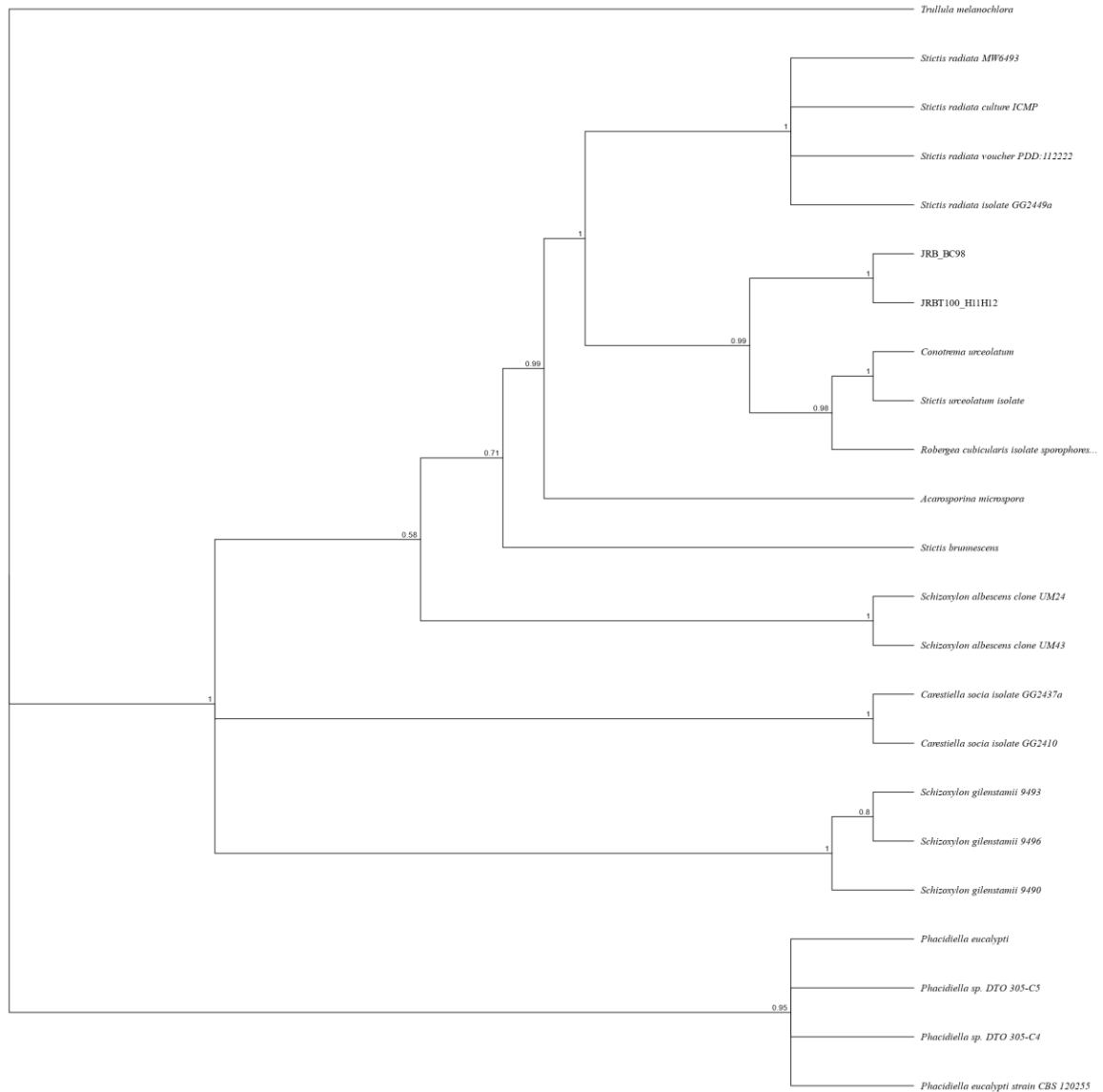


Figure 21. Phylogenetic relationships comparing 351 bp ITS rDNA molecular data for 23 ascomycetes including *Robergea albicedrae* samples, JRB_BC98 and JRBT100_H11H12. This tree was generated from 50% majority rule consensus of 2,500,000 trees analyzed with MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) Bayesian analysis using Markov chain Monte Carlo sampling within Geneious 2019.2.1. *Phoma* sp. was set as the outgroup and rooted so the outgroup would be a monophyletic sister group to the ingroup. Posterior probabilities presented above each branch, MCMC chain length = 1,100,000, subsample frequency = 200, and heated chains = 4.

IV. DISCUSSION

In Situ Coverslip Observations

The diversity of fungi and lichens on plant surfaces has been an area of interest for many years. Methods of studying epiphytic lichens were developed by Sanders (2005), who used plastic coverslips as an *in situ* substrate. This approach has not been used to study endophytic, corticolous, or lignicolous fungi, however the problem of being able to microphotograph the progression of colonization of fungi is similar to that encountered in the study of tropical lichens. Using a protocol modified after Sanders (2005), coverslips were placed on the bark of Ashe juniper trees in order to gather data on the hyphal morphology and habit of *Robergea albicedrae* and to document perithecial formation and possible interaction with an algal constituent in terms of possible lichenization.

Coverslips were collected and photographed every three months for 17 months after being attached to Ashe juniper trees, resulting in 108 coverslips collected. The coverslips showed significant colonization by fungi and algae, along with a myriad of spores, pollen, invertebrates, and dust. The appearance of multiple stages of fungal growth on the cover slips indicates that this substrate is a good surface to document the development of fungi. Unfortunately, mature perithecial formation was not documented in this study, perhaps due to the complex relationship between the fruiting structures of *R. albicedrae* and the host tissue, or possibly due to inadequate time *in situ*.

The green alga *Trebouxia*, identified by morphology and molecular sequence data, was observed growing on the coverslips, both free-living and in association with fungal hyphae. This result is similar to that observed by Sanders (2005), despite other

studies describing the occurrence of free-living *Trebouxia* as a rare and exceptional event (Degelius 1964).

It would seem that the smooth surface of the plastic coverslip would be disadvantageous to colonization of fungi, and it was observed that the stages of development depended on length of time after initial placement: the longer the coverslip was in place, the more complex and diverse was the fungal and algal growth. It seemed as if the fungal growth followed a grid like pattern that corresponded with the mesh/burlap weave pattern. Dust, pollen, and other detritus would affix along these lines and allowed the fungal spores to attach there and then germinate. It is possible that the detritus might have also served as a nutrient source for growing hyphae. Increased detritus yielded an increase in fungal growth, but also hampered observation as the coverslips were less transparent and details were more difficult to record.

Fungal spores present on the coverslips were numerous and diverse and included those of common molds and plant pathogens such as *Fusarium* sp., *Aspergillus* sp., *Beltrania* sp., *Alternaria* sp., and *Pithomyces* sp., along with others. The coverslips seemed to be a suitable substrate to document these spores, however inferences cannot be made as to whether they are fungal endophytes, saprobes on Ashe juniper, or simply passing through while being transported via the wind. *Robergea albicedrae* spores were found on the coverslips, either having been discharged from perithecia on the trunk and landing on the coverslips or having been expelled during a rain event and washed onto the surface of the coverslip. Spores of *R. albicedrae* were not found commonly on the coverslips and were encountered more frequently later in the observation period. Increasing the duration of the experiment might be useful in getting images of

germinating spores. In an effort to document perithecial formation, a series of time lapse images over a year might provide useful information about spore dispersal, perithecial growth, and expansion of the pruina.

Anatomical Observations

Until now, the only available observations of *Robergea albicedrae* were line drawings from the original species description and an updated review of the order Ostropales (Heald and Wolf 1910; Sherwood 1977). These authors provided valuable information about perithecial, asci, and spore morphology, however little data was available on other taxonomic features and the habit of the fungus. Using detailed microphotographs and various preparation techniques, data was collected with the goal of understanding more about *R. albicedrae* and its interactions with the wood of *J. ashei*. It has been proposed that *R. albicedrae* is a possible parasite and it is currently described as a fungal endophyte; however it has also been suggested that it may have a facultative relationship with a green algal photobiont (Sherwood 1977). The family Stictidaceae, in which *Robergea* is nested, includes some species were described as saprophytic (*Stictis* spp.) while others that are morphologically identical except for the presence of algae in the thallus (*Conotrema* spp.) were described as being lichenized. Wedin et al. (2004, 2005) and Lumbsch and Leavitt (2011) have documented three cases where species of Stictidaceae have displayed optional lichenization.

Macroscopic images of fungal growth on Ashe juniper were obtained after fresh collection. The fungal growth of *R. albicedrae* varies depending on the substrate (wood of twigs or bark of trunk). No one preparation technique provided all the information needed: fresh cuts, embedded sections, thin sections, and a variety of stains were all

useful in collecting data about the structure of *R. albicedrae*. The safranin stained samples gave good details on the perithecium, corrupted wood cells, and hyphal growth of the fungus, while CLSM was able to show details of the fungus and spores deep in the wood tissue, and images from coverslips collected from the trees were useful in showing fungal hyphae growing in conjunction with algal cells. Observations of the wood-fungus interaction required that the fungus be stained differentially from the wood cells due to the strong autofluorescence of wood across a wide range of wavelengths (Xiao et al. 2000), therefore, a fluorescently tagged lectin stain that could bind to chitin and not cellulose was important for viewing the fungus. While no thin sections were encountered that documented an optional lichenization for *R. albicedrae*, this mode of nutrient assimilation cannot be ruled out. Observations of fungal and algal interactions in *Conotrema* need to be studied and then compared to those of *R. albicedrae* in order to elucidate the amount of interaction occurring between the fungus and alga.

Difficulties arose in keeping the fragile bark intact when thin sectioning. It was difficult to differentiate between algae growing on the surface of the bark on the fungus and with the fungus. In the future, observations using astra-blue as a co-stain with safranin could help determine if the fungus has lignin degrading capabilities and how the wood in the twig compare to that of wood covered in bark (Srebotnik and Messner 1994).

Pruina Composition Test

The goal of this investigation was to determine the composition of the white powder that is present on the surface bark of *J. ashei* trees. Within these white patches are the only place the fruiting structures (perithecia) of the fungus *Robergea albicedrae* can be found. No tests have been done previously to determine the chemical or

biological composition of this white powder, despite it being referred to as a pruina, which implies it is composed of calcium oxalate. However, when viewed under the microscope, long threads of bleached wood tissue can be seen, indicating it may be a layer of dead and bleached wood cells and fungal hyphae.

The process of deposition and the function of calcium oxalate in fungi (including the mycobiont of lichens) and plants has been broadly studied and debated. It has been shown that calcium oxalate has a metabolic role in regulating water in some lichens and can prevent herbivory by invertebrates (Edwards et al. 2004). Some plants and fungi precipitate calcium oxalate crystals in order to detoxify when excess calcium is present (Fink 1992). Garty et al. (2002) found no difference in the presence of calcium oxalate in clean air versus polluted sites, implying that the source of calcium oxalate crystals is not based on air pollution, but rather substrate chemical composition or by entering the system as calcium carbonate in suspended dust particles derived from wind eroded limestone substrates.

In this study the samples tested using FTIR spectroscopy had 11 main peaks in their IR spectra. The presence of a peak at wavenumber 1315 cm^{-1} (Figures 13, 14, 15) indicated the presence of calcium oxalate monohydrate. There were no peaks for calcium oxalate dihydrate (weddellite), which would have been found at 1326 cm^{-1} . There is also a major peak at 1615 cm^{-1} which can be identified as the calcium oxalate C-O stretch (Palacio et al. 2014).

All three spectra show two main peaks in the range between 590 and 690 cm^{-1} , these corresponding to the spectral fingerprint of gypsum (Palacio et al. 2014). This could be due to precipitation of atmospheric dust containing gypsum or the reaction of

calcium carbonate with acidified rainwater, which would produce gypsum. Studies have found that areas with higher industrialization had higher incidences of gypsum deposition on plant and lichen surfaces. Gypsum can also be linked to a biological process of calcium leaking from injured cells and forming a neutralizing reaction with acidified water on the surface of the plant (Garty et al. 2002). Palacio et al. (2004) noted that plants can accumulate gypsum crystals as a way to remove an abundance of calcium and sulfur molecules and that the size and volume of calcium oxalate crystals are responsive to changes in soil chemistry.

The white powdery patches on the upper surfaces of the bark of Ashe juniper that have been described as patches of fungal growth by some and loosely as pruina by Sherwood (1977) are indeed a pruina, consisting of calcium oxalate monohydrate crystals and bleached bark cells. Efforts to discern the composition of these white patches and differentiate them from a possible layer of dead fungal hyphae were successful. Supporting evidence from FTIR spectroscopy indicates the presence of calcium oxalate monohydrate, calcium sulfate, water, and other organic compounds on the bark. It has been noted that epinecral layers tend to be more developed in areas exposed to higher amounts of sunlight, possible as a defense against UV radiation (Heidmarsson 1996). Initial observations of the variation in the size and thickness of the pruina on Ashe juniper does not seem to indicate that they are based on exposure to light, as shaded and exposed areas tend to have similar-sized patches of white.

The presence or absence of pruina is a common and important taxonomic character and is frequently used to describe white, “frosty” surfaces found in plants, fungi, and lichen. However, efforts should be made to use caution with the term in order

to accurately describe these surfaces, and tests should be done in order to ensure pruina is a term used to describe the presence of calcium oxalate crystals and not just sun bleached tissues or other materials in epinecral surfaces. Calcium oxalate monohydrate is more stable than calcium oxalate dihydrate, the latter of which tends to disappear from the system if moisture is present (even humidity). However when conditions are very dry, calcium oxalate dihydrate tends to be found in greater ratio to calcium oxalate monohydrate (Frey-Wyssling 1981). Although the samples were collected in April 2019, when there was abundant moisture, the peaks above 3000 cm^{-1} are due to O-H bonds in the water and cellulose molecules (Palacio et al. 2014). Wadsen and Moberg (1985) state that the presence of calcium oxalate is most likely a means of ridding the fungus of excess calcium. The presence of only calcium oxalate monohydrate associated with *R. albicedrae* is likely because this fungus grows in more humid areas (Wadsen and Moberg 1985).

Isolation of Pure Fungal Cultures

Some of the pure cultures could not be identified based on the lack of complete 18S sequence data available for many fungi and the lack of fruiting structures present when the cultures were dissected and studied for morphological information. Table 6 summarizes the distribution of pure cultures among fungal genera, orders, and classes. Note that percent abundance is based on genus rather than species. Of the total number of isolations attempted by grinding the perithecia, dissection of the perithecia and natural spore dispersal, 53%, 93%, and 33%, respectively, were successful. The resulting pure cultures, based on the type of medium used, was broadly comparable with 44% being grown on a variation of bark extract and 56% on a variation of MEA. Many of the

fungi identified were common fungal contaminants (*Alternaria*, *Cladosporium*, *Fusarium*, *Epicoccum*), fungi that are normally present on plant and soil surfaces, in addition to their spores being commonly found as internal air contaminants. Despite efforts to remove contamination using a 24-hour water wash and excising internal tissue during plating, these contaminants were inevitably present. Surface sterilization would not be appropriate in attempts to culture *Robergea albicedrae* until more knowledge is obtained about how the hyphae grow and interact with the host tissue, to insure avoiding the inadvertent absorption of treatment chemicals that could impair fungal growth.

Crittenden et al. (1995) found that *Ostropales* had a high success rate in terms of culturability, and this inspired the current attempt to culture *Robergea albicedrae*. This fungus had not been cultured previously and little information existed on what the mycelium looked like or if culture conditions could mimic the host interaction it has with *J. ashei*. After the extraction of DNA from 67 pure cultures and sequencing 112 different fungal amplicons, one ITS sequence matched the family Stictidaceae when searched against the NCBI nucleotide database. This sample was pulled from a small (3 mm) white colony that was very slow growing. Sherwood (1977) described the hyphae of *R. albicedrae* hyphae as possibly being light tan, so having a white colony yield sequence data for *R. albicedrae* was surprising. Explanations might include that the fungi have a darker color when growing on wood tissue due to the number of phenolic compounds, resins, and other chemicals found in wood. The sample was produced by allowing a washed perithecium to disperse its spores naturally upward onto the agar medium containing 100% bark extract. Most lichens and many fungi discharge their spores forcibly (Hawksworth and Hill, 1984) so following this approach seemed reasonable and

might also help to limit contamination from the air on the agar surface as it would be facing down during inoculation. A possible explanation as to why more plates did not support the growth of *R. albicedrae* might be that their spores discharge when wet, as a mucilaginous exudate with the spores inside. The water wash might have released most of the spores, leaving very few to inoculate the plates after. Future attempts to culture this fungus could include skipping the water washing step and having some inoculations where the spores are dispersed downward instead of upward.

When the perithecia were collected from bark, they were brought to the lab and used immediately. This timeliness was to prevent desiccation and contamination of the fungal tissue, however, it was not possible to know if the spores had already dispersed on the tree before being harvested. Because the method of spore dispersal had success in culturing *R. albicedrae*, future attempts would increase the number of perithecia sampled. In relation to this, sampling the fungi during different seasons, sites, and tree space would provide physiological data on how the fungi viability responds to changes in air moisture, temperature, and host moisture content.

Along with efforts to culture and sequence *Robergea albicedrae*, a myriad of other fungi were identified. The trees sampled only exhibited the patches of white that are normally associated with *R. albicedrae* and were visually asymptomatic for plant disease, however, a range of endophytic ascomycetes and basidiomycetes, including yeasts, were present. These fungi had varying rates of growth and nutrient preferences in culture. Many studies have attempted to characterize the mycoflora occurring on different plants and in different systems around the world, although none have characterized that of *Juniperus ashei* (Diamandis and Perlerou 2001; Tejesvi et al. 2005;

Verma et al. 2007; Gehlot et al. 2008). Samples were taken from bark and twigs, indicating that many of the fungi identified may be xylotropic endophytes. Petrini et al. (1993) have noted that many of these bark and wood inhabiting fungi provide a secondary metabolite advantage to the plant by being antimicrobial. Expanding this study by sampling many sites on the same tree (each site a different ecosystem) and comparing these sites between populations of trees would yield a more complete picture as to the level of biodiversity present in the mycoflora of Ashe juniper.

Molecular Assessment

The goal was to compare sequence data for *R. albicedrae* from 18S SSU rDNA and the ITS 1 and 2 regions using phylogenetics. Fungal samples from the bark of Ashe juniper trees were processed for DNA extraction using an amended CTAB protocol because standard fungal DNA extraction kits were unsuccessful. This was due to the high volume of inhibitory chemicals present in the plant and fungal tissue. The ITS region was sequenced using raw environmental DNA samples, but it was of low quality due to other fungal contaminants. Because these environmental samples contained many fungi, PCR products were cloned. Cloning helped to isolate individual sequences that were clean. Using this technique 18S sequence data was isolated from *R. albicedrae* as well as a host of other fungi. There is a high diversity of fungal endophytes present on Ashe juniper bark.

The lack of success in early amplifications of the DNA samples was due to using primers that were not well matched for the *R. albicedrae* samples. The nssu131/NS4 primer set had the most success in amplification once the thermocycling conditions were optimized. Also, despite using the CTAB protocol to limit inhibitors, samples had to be

diluted at various concentrations to ensure proper amplification.

The initial uncloned samples that were able to be sequenced at the ITS region were compared to the NCBI database using a BLAST search and showed 74% and 71% similarity to *Robergea cubicularis*. *Robergea cubicularis* is the only taxon in the genus with molecular data present in GENBANK. Also, the list of the top 30 hits for both sequences contained only members of the order Ostropales, with most falling within the family Stictidaceae. Due to the lack of sequence data available in this database, especially within the genus *Robergea*, this was encouraging for the placement of these two species in the same genus and within the family Stictidaceae. These observations are consistent with morphological data that has been presented based on ascus formation and spore shape. More analysis needs to be done to compare differences between *R. albicedrae* and other members of the family Stictidaceae, like *Stictis* and *Acarosporina*.

Cloning samples were able to produce *R. albicedrae* sequence data for the 18S SSU region, and comparisons with other taxa in GenBank show the same rate of similarity with other species in the family Stictidaceae. *Robergea cubicularis* could not be compared at this region due to lack of sequence data, however future studies to compare all *Robergea* species on the molecular level would help to delineate this genus and confirm its placement within the family Stictidaceae.

Phylogenetics

For the phylogenetic analysis, 18S and ITS rDNA molecular data was compiled for 58 fungal taxa, aligned, and analyzed using neighbor joining distance and Bayesian methods. The goal was to compare *Robergea albicedrae* to other members of the family Stictidaceae and within other orders in the phylum Ascomycota. There has been much

discrepancy in the familial placement of *Robergea*, although current morphological work places it in Stictidaceae. This placement was strongly supported based on the trees produced using two common phylogenetic techniques and the analysis of the 18S and ITS regions.

The neighbor joining distance analysis with bootstrap consensus (Figure 18) showed a tree topology that was consistent with the Bayes tree (Figure 19), however bootstrap support values were low not only within family groupings but also between orders (Figure 18). Neighbor joining methods work well when the data has few changes over time and the rates of change are equal for all evolutionary lineages present, however when these assumptions are violated frequently the methods result in error (Felsenstein 1978, 1981). Comparing the entire phylum Ascomycota down to species is challenging, as when ITS data is compared beyond the species level, the level of substitutions in the data will be great. Despite the variability between individual sequences, neighbor joining methods group taxa into the correct families for the most part. The ITS region is too variable for class wide comparisons, but as shown in Figures 20 and 21, there is strong support for the placement of *Robergea albicedrae* in the family Stictidaceae. This placement was also supported by the neighbor joining tree for both the 18S and ITS data.

The analysis method that produced trees with the most phylogenetic support for the correct taxonomy for the known OTUs, according to current literature, was Bayes. Most of the current literature that addresses phylogenetic assessments for the phylum Ascomycota uses Maximum Likelihood and Bayesian analyses (Padovan et al. 2005; Schoch et al. 2009; Miadlikowska et al. 2014; Yarza et al. 2017). The Bayes topologies (Figures 19 and 21) split the sequences into two distinct clades, Ostropales and

Teloschistales. *Wiesneriomyces* is earlier diverging in the phylogeny but still grouped together with the rest of its clade with strong support. All the phylogenies show *Robergea* being one of the latest diverging taxa. As the tree elevation increases there is molecular and morphological data that Ostropales should be considered one of the later diverged orders (Sherwood 1977; Lücking et al. 2004b; Lutzoni et al. 2004; Schoch et al. 2009), although this is not supported by any of the analyses provided in this study due to an insufficient breadth of taxa.

The ITS region was chosen because *Robergea cubicularis*, which is morphologically related to *R. albicedrae* (Sherwood 1977), had only an incomplete 18S SSU region and a full ITS region in GenBank. To improve the quality of the sequence data used, analysis of a more conserved area in the genome should be used to construct ordinal level trees and ITS data used to tease out species level relationships. Currently used genes for ascomycete research include ITS, SSU and LSU rDNA, SSU mtDNA, and the RNA polymerase II LSU 1 and 2 (Lutzoni et al. 2001; Lutzoni et al. 2004; Miadlikowska et al. 2014). The current study suggests strong support for the nesting of *Robergea albicedrae* in the family Stictidaceae. More analyses will be conducted to develop a more accurate order-wide phylogeny using 18S data, and to incorporate more members of the genus *Robergea* into the phylogenetic tree for Ascomycota.

It was the goal of this research to collect new information about *Robergea albicedrae* at both the morphological and molecular level. Gathering information about how this fungus grows and reproduces was paramount along with molecular information to help to understand familial relationships. As an interesting and important ecological tangent, uncovering the diversity and complexity of the other taxa growing in relation

with *R. albicedrae* on the bark of Ashe juniper only emphasized the richness of information that has yet to be uncovered in terms of ecological associations and community assemblages present on tree bark.

APPENDIX SECTION

JRB_BC1

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JRB_BC56

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JRB_BC57

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JRB_BC58

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JRB_BC59

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JRB_BC61

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JRB_BC62

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JRB_BC65

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JRB_BC66

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JRB_BC67

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JRB_BC69

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JRB_BC70

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JRB_BC72

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JRB_BC73

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JRB_BC74

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JRB_BC75

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JRB_BC76

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JRB_BC77

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JRB_BC78

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JRB_BC79

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JRB_BC80

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JRB_BC81

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JRB_BC82

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JRB_BC83

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JRB_BC84

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JRB_BC85

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JRB_BC86

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JRB_BC87

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JRB_BC89

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JRB_BC90

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JRB_BC91

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JRB015_81_89

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JRB002_33_41

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