Identification and DNA taxonomic analysis of a library of endophytic fungi

by

Ryleigh A. Stack

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Supervisors: Dr. Christopher A. Gray, Department of Biological Sciences and Department of Chemistry

Dr. John A. Johnson, Department of Biological Sciences

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ABSTRACT

Endophytes represent a largely untapped source of natural products. Despite a growing body of research, data and knowledge relating to endophyte biology and chemistry, one of the difficulties in endophyte research remains the accurate identification of endophytes. The advancements and development of molecular methods have provided researchers with tools that allow them to obtain an identification based on the endophyte's DNA sequence, rather than its morphological and/or phenotypic characteristics. In the present study, the DNA extracted from 155 endophytes was analyzed following a DNA taxonomy methodology and compiled to give phylogenetic trees to obtain identifications based on the molecular properties of the endophytes, rather than their morphology. Of the 155 endophytes; 57 were identified to the species level, 65 to genus, 5 to class, 2 to subdivision, 10 to order, 15 to family, and 1 to subclass.

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STATEMENT OF RESEARCH CONTRIBUTION

The endophytic fungi analysed for this project had all been previously collected, and the DNA had been extracted and sent for sequencing before the commencement of my honours research project. I retrieved all genetic sequences from Genome Québec in FASTA format, which were then compiled to obtain the required multiple sequence alignments. Maximum-likelihood trees were built for subsets of the data as well as the entire dataset. Once completed, the phylogenetic trees were analyzed to determine a breakdown of the isolates and determine the highest level of classification that could be obtained as an identification using the DNA taxonomy approach.

Table of Contents

List of Figures

List of Symbols, Nomenclature or Abbreviations

BLAST: Basic local alignment search tool

DNA: Deoxyribonucleic acid

FASTA: FAST-All

ITS: Internal transcribed spacer

MEGAX: Molecular Evolutionary Genetics Analysis version X

MSA: Multiple sequence alignment

MUSCLE: Multiple sequence comparison by log-expectation

NPRG: Natural Products Research Group

UNBSJ: University of New Brunswick Saint John

Introduction

Natural products are chemical compounds produced by living organisms as a result of their primary and secondary metabolisms.[1] Natural products are interesting because of their biological activity, their novel chemical structures and the high diversity observed in their structures. Since their first discovery over 200 years ago,[2] natural products have played an integral role in many of fields of research including pharmaceuticals and therapeutics,[3,4] agriculture,[5] and industrial uses[6] with importance in the development of novel therapeutics and naturally derived drugs.[7] Notably, natural products have played a significant role in discoveries relating to antibiotics, immunosuppressants, and cancer drugs to name but a few.[2] Although natural products can be isolated from numerous sources, plants have been, and continuing to be, central to isolation efforts as they represent an important source of natural products and bioactive metabolites. [8-13] Despite this, the increasing need for the discovery and development of new therapeutic products have resulted in the investigation of new sources and led to the study of endophytes as a source of natural products.[14]

An endophyte is a fungus that lives in plant tissue for part of or all of its life without causing any symptoms of disease.[15] While endophytes may serve many roles within the plant, for example defending against pathogens and serving various roles throughout the plant's life cycle,[16,17] it is the natural products that these fungi produce that are of interest to chemists.

Endophytic fungi are incredibly diverse, both morphologically and physiologically, with the physiological diversity allowing them to be a source of diverse bioactive metabolites.[18] In addition, there are many endophytes; as of 2015, there were no recorded plant species in existence without a fungal endophyte.[19] Although the number of possible species of endophytes

is unknown, fungi represent the second largest group of eukaryotic organisms with estimates ranging from 1.5-5.1 million species,[20,21] thus representing a wide range of possible extant species, of which, the majority have not been isolated or studied.

As the discovery of natural products has grown to encompass endophytes, the identification of endophytic fungi is important for determining their application as literature reports on previously identified endophytes exist; once identified, researchers have a better idea of what the endophyte should be studied for, and if the endophyte could lead to the discovery of new chemistry. Traditionally, identification was performed based on morphological structures. Morphological identification is carried out based on the reproductive structures of the fungus, whether it is producing sexual spores or conidia, and a number of phenotypic characteristics the fungus may produce. However, identification based on morphology alone is subject to several limitations meaning that incorrect identification occurs readily as the morphological characteristics can be misleading due to hybridization,[22] cryptic speciation,[23] and convergent evolution,[24] all of which can be problematic. In addition, endophytic fungi often do not reach the sexual state or sporulate in culture,[25] thereby not giving rise to the observable phenotypic characteristics required for identification such as colony appearance which includes the colony's form, elevation, and margin. Finally, in the absence of the sexual spores or conidia, the phenotypic characteristics present show high plasticity[26] making identification troublesome at best. Fortunately, the development of two molecular techniques; DNA barcoding, and DNA taxonomy,[27] have been progressively applied to the identification of endophytes[24,28,29] presenting researchers with alternate identification methods.

DNA Barcoding

DNA barcoding uses short standardized regions of a DNA sequence, typically 400-800 base pairs in length, to identify an organism. The internal transcribed spacer region, or ITS region is the official DNA barcode marker for fungi, with several studies having found it to be associated with the highest probability of correct identifications across a broad group of fungi.[30] As such, it is typically the ITS region or sub-regions that are amplified and utilized in the process of DNA barcoding.[31] The ITS sequence is uploaded into an online database such as GenBank which uses a BLAST©[32] search tool or UNITE[33], which both present the user with a list of top identification "hits" within the system based on the similarity in the sequences housed in the database and the unknown sequence, and the gaps that exist within the sequence. Although this approach has proven to be a robust source of identification, there are limitations that are associated with its use.

Given that the unknown fungal DNA sequence is entered into an online database, this approach is dependent on the accuracy of the sequence identifications that have been previously input into the database. While there are a number of reference sequences that serve as comparisons for barcoding, not all fungal species have a reference sequence that has been made accessible.[34] Moreover, there are several unpublished sequences that have been added to the databases,[35,36] which may decrease the validity of the identification as these sequences may be incorrect and unverified leading to the improper identification of the unknown. Finally, while the ITS region has been accepted as the DNA barcode marker for fungi, it does not work well for highly speciose genera that have a high number of species within it; although there are gaps within most DNA sequences, they are small or non-existent when comparing between highly

similar species. This limitation includes the genera *Aspergillus* and *Penicillium*[37,38] as they both have very narrow barcode gaps if any at all. Since these genera have typically yielded important natural products, this limitation is severe for those in this field of research.

DNA Taxonomy

DNA taxonomy differs from DNA barcoding in that it takes the unknown sequence and places it into an evolutionary framework with other sequences, both known and unknown rather than using a database for comparison.[39] In placing the unknown sequence into this type of framework, it allows you to see within which phylogenetic clade or group it falls, and what this means taxonomically. This provides an opportunity to determine the unknown's lineage and, hopefully, an identification.[40] This framework can also be called a phylogenetic tree which is built using several sequences that have been aligned in a multiple sequence alignment, and then formed into a tree for researchers to read and interpret.

Although both techniques were developed and proposed at the same time,[27] DNA taxonomy has not been employed as commonly as DNA barcoding. Being cognizant of this information, the objective of this research was to examine the University of New Brunswick Saint John's (UNBSJ) Natural Products Research Group's (NPRG) library of fungal endophytes (isolates) using a DNA taxonomic approach and determine a breakdown of the isolates within the library. The NPRG endophyte library is made up of 280 isolates, however, for 125 of the isolates multiple attempts to extract and amplify DNA were unsuccessful, so the completion of this project was carried out on 155 endophytes.

Materials and Methods

All fungal endophyte cultures used in this research were previously isolated from their host plant species by members of the Natural Products Research Group (NPRG) and DNA from the ITS region was isolated, amplified by PCR and sent for sequencing at Genome Quebec. All sequences were obtained from Genome Québec in FASTA format and organized based on their collection within the entire library for further analysis and use.

Multiple Sequence Alignment

Compilations of the isolate sequences were uploaded into the online multiple sequence alignment tool, MUSCLE.[41,42] Output format was set to FASTA with an output tree following the first iteration, and the sequence alignment was run. The alignments were then saved and exported for further use.

Phylogenetic Tree Building

The multiple sequence alignments (MSA) were imported into Molecular Evolutionary Genetics Analysis (MEGA) version X.[43] Each alignment was used to create a phylogenetic tree using the phylogenetic and evolutionary analyses within MEGAX. Once imported into the software, maximum likelihood trees were built following the Tamurai-Nei method using a bootstrapping value set to 1000 repetitions. This method was repeated for each data set within the library, and the combined dataset.

Results

Upon completion of the maximum-likelihood phylogenetic trees (Appendix 3), the trees were examined to determine the identification of the endophytic isolates. It was determined that of the 155 isolates that were analyzed 147 belonged to the division Ascomycota, while 8 belonged to the division Basidiomycota (Figure 1). More in depth analysis revealed that 57 isolates were identified to the species level, 65 at the genus level, 15 to family, 10 to order, 1 to subclass, 5 to class, and 2 to the subdivision level (Figure 2). The 122 isolates that were identified to the genus and species levels represented 49 distinct genera, with the majority of isolates (20) being reported within the genus *Penicillium* (Figure 3). Finally, the 57 isolates that were identified to the species level comprised 34 distinct species, of which *Aspergillus fumigatus* (7) was the most commonly identified (Figure 4).

Reading phylogenetic output

In analyzing the phylogenetic tree output, it was possible to determine identifications for isolates that had not been fully identified during previous attempts. Isolates that were grouped into clades, exhibited strong support values, or had similar distances from a common ancestor were identified based on the isolates they were grouped with. An isolate that was identified to the species level in this manner was JAJ1-093 as it formed a monophyletic group with four other isolates that had been previously identified as *Paraphaeosperia neglecta* (Figure 5).

Figure 1: The taxonomic distribution of the NPRG endophyte library (n=155) at the division level based upon DNA taxonomic analyses of the ITS DNA region.

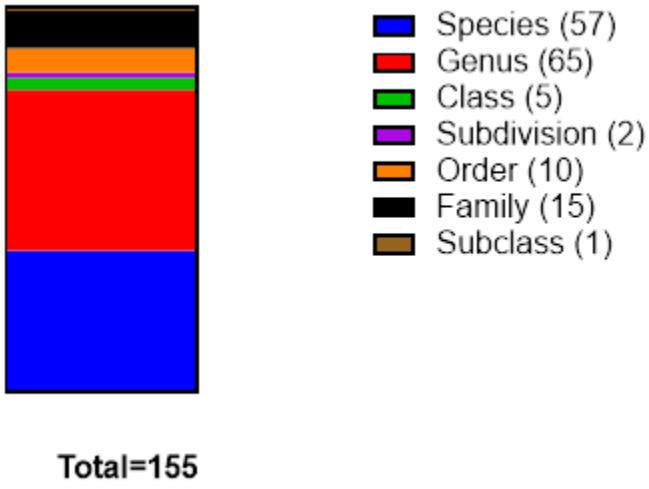

Figure 2: The taxonomic distribution of the NPRG endophyte library (n=155) based on level of identification obtained using DNA taxonomic analyses of the ITS DNA region.

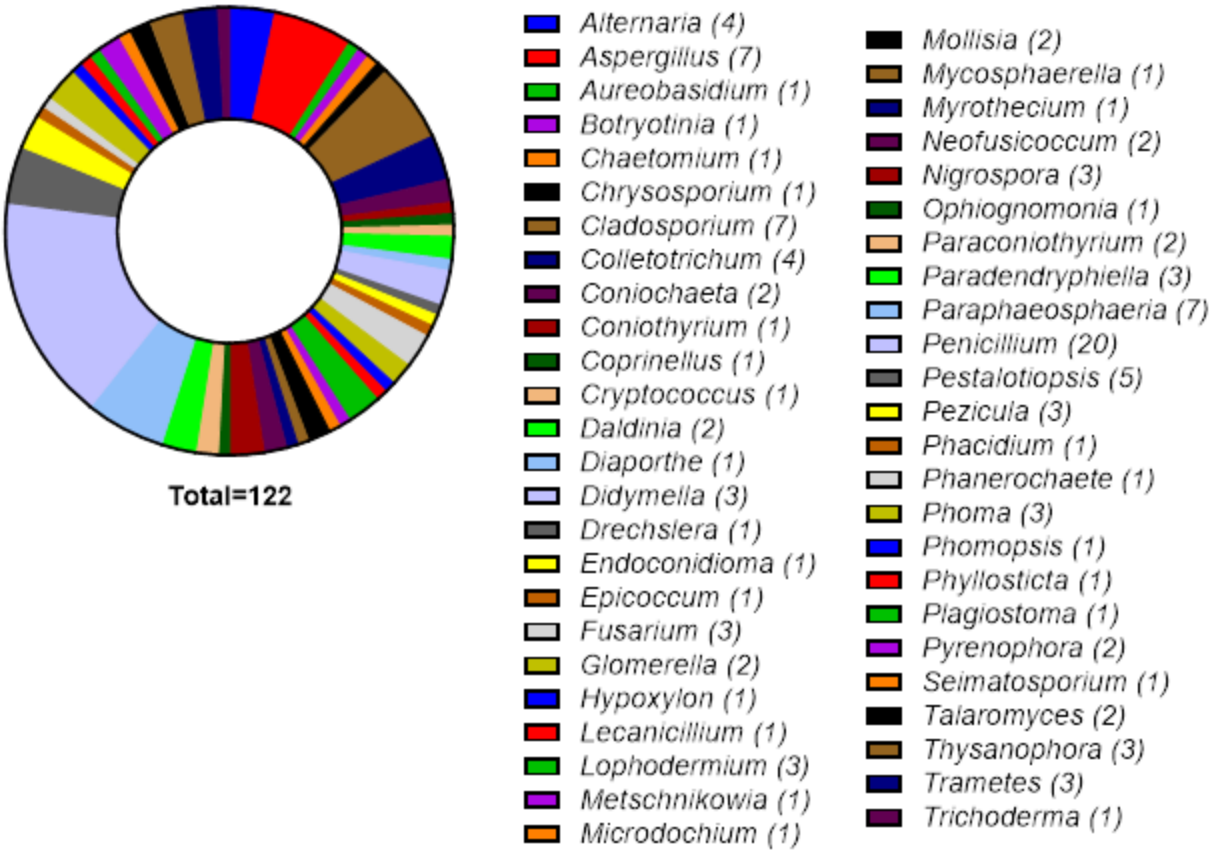

Figure 3: Taxonomic distribution of the NPRG endophyte library (n=122) at the genus level based upon DNA taxonomic analyses of the ITS DNA region.

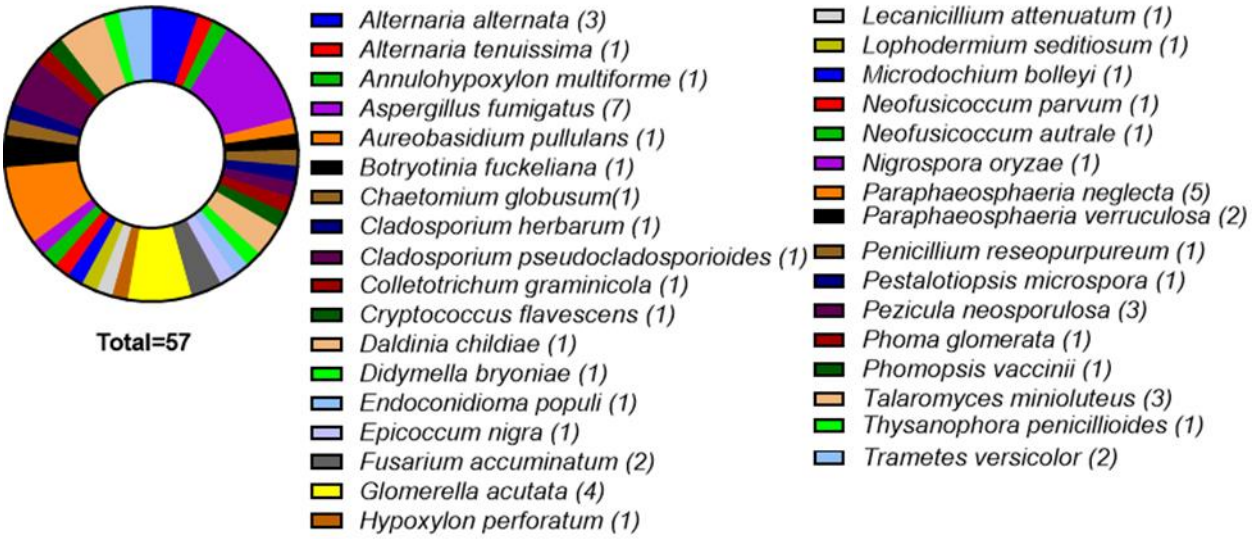

Figure 4: Taxonomic distribution of isolates identified at the species level (n=57) within the NPRG endophyte library absed upon DNA taxonomic analyses of the ITS DNA region.

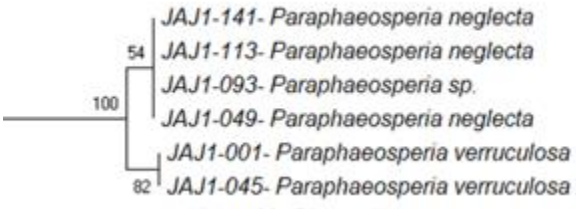

Figure 5: Example of phylogenetic output obtained from MEGA version X used to identify isolate JAJ1-093 as *Paraphaeosperia neglecta* which had previously been identified as *Paraphaeosperia sp*. by a BLAST search.

Discussion

In the search for natural products, plants have served as a source of bioactive compounds for centuries.[44] The knowledge that exists relating to herbal remedies has developed over several millenia, with evidence stemming from ancient Egypt and the use of natural resources,[45] and has led to the discovery of many effective drugs.[46,47] Globally, the use of plants for medicinal practices was important long before the development of technology and engineering that has

allowed researchers to identify the active constituents. [48,49,50] The development of technology that has occurred in the late 20th and early 21st centuries, has allowed researchers to better understand how plants have contributed to remedies for ailments such as tuberculosis,[51,52] and understand their roles in several complex medical ailments that have proven to be difficult to treat.[53] While plants have been a plentiful source of natural products, there still exists a resistance of bacteria and viruses to medicine currently available[54] which has highlighted the necessity for continuing and, in some cases, prioritizing the discovery of novel natural products to counteract the observed resistance. While research and isolation efforts continue with plants, they have also grown to include a number of other reservoirs, such as endophytic fungi, as a potential source of natural products.[19]

Although first described in 1809 by German botanist Johann Hienrich Friedrich,[2] endophytes were not immediately recognized as a source of natural products; the field of endophyte biology is therefore a relatively new discipline with research beginning in the late 1970's[55,56] leaving much knowledge to be discovered. Despite this, more recent research has found that endophytes act as a source of novel bioactive metabolites and organic molecules such as alkaloids, phenolic acids, quinones, terpenoids, peptides, steroids, aromatics, hydrocarbons, and others that have the capacity to serve as candidates for antimicrobial, anti-insect, anticancer, and many more properties.[44,57,58] Additionally, many of the biologically active compounds mentioned above have been classified as antibiotics, antioxidants, anticancer agents, volatile antimicrobial agents, immunosuppressive compounds, plant growth promoting agents, and insecticides.[58] These promising features, along with the high diversity of endophytes[18] has supported the consideration of endophytes by discovery researchers as a source for potentially interesting natural products.

In the study of natural products, it is often difficult to find a product that exhibits both new chemistry and bioactivity, with many natural products exhibiting novel chemistry with no bioactivity, or unreported bioactivity for known chemical structures. In many research groups, as well as at the NPRG, several prioritization methods have been developed to attempt to target isolates that exhibit both new chemistry and bioactivity, rather than one or the other. These have included metabolomic methods and bioactivity profiling that examine the chemical properties of the isolates, but a research project focused on the molecular properties of the endophytes had not previously been completed. In applying this technique, it was possible to determine a more comprehensive breakdown of the NPRG library and identify isolates to the genus or species level based on the groupings that were observed in the phylogenetic output that was generated, which resulted in a successful application. Despite the success with identification that was obtained, it was not possible to identify all endophytes to the species or even genus level. DNA taxonomy builds off the sequences that are included in a phylogenetic tree and the possible inclusion of reference sequences, to determine a possible identification based on the relatedness between the sequences. As such, the rate of success is dependent on having sequences for similar endophytes within the tree. By undertaking the molecular analysis, similar sequences are placed into groupings, i.e. clades, that identify the most common recent ancestor shared as represented by a node in the tree, and the distance from that ancestor can help in determining the likeness of endophytes along with the confidence value that is associated with the placement in the final tree.[26] Although there were isolates that could not be further identified using the DNA taxonomic approach on this dataset, a larger more diverse dataset or the inclusion of additional reference sequences would improve the success of the technique, as the strength of the phylogenetic output is reliant on the number of sequences that are within it.[26]

The NPRG endophyte library contained endophytes that were expected given their past documentation as both prevalent endophytes and plant pathogens especially those within the genera *Cladosporium,*[59] *Colletotrichum,*[60] *Fusarium,*[61] and *Mycosphaerella*.[62] Although most endophytes were expected, there were several that were found to be opportunistic human pathogens rather than having much evidence as a plant pathogen; species within the genera *Aspergillus*[63] and *Paraconiothyrium*[64] have all been linked to human infections and disease. In addition to the endophytes within the collection that were found to be human pathogens, *Aureobasidum*[65,66] and *Chaetomium*[67] are are both genera that have been found to include species that act as a plant defense to invading pathogens. Finally, three endophytes were identified within the *Paradendryphiella* genus which was notable as this genus is known as a marine fungus rather than an endophyte,[68] although these endophytes were isolated from a marine environment they remain notable as they represent an uncommon genus.

Of the isolates that were identified to the species level, seven were identified as *Aspergillus fumigatus*. A filamentous fungus, *Aspergillus fumigatus* is a prevalent airborne pathogen that can cause severe harm to humans, especially those that are immunocompromised.[63,69,70] Despite its status as a human pathogen, *Aspergillus fumigatus* has yielded several natural products including two alkaloids; 9-deacetylfumigaclavine C (1) and 9-deaceteoxyfumigaclavine C (2) the latter of which showing cytotoxicity against human leukemia cells that was comparable to drug treatment options that are currently prescribed,[71] as well as ruakuric acid that belongs to the family of natural products called the chromans.[72] In addition to the isolates identified as *Aspergillus fumigatus,* 20 isolates were identified as belonging to the genus *Penicillium* which has been a source of diverse bioactive metabolites from alkaloids and polyketides with plant growth promoting qualities[73], to quinazilones such as Verrucine F which

has previously been isolated from *Penicillium verrucosum*.[74] Although both the *Aspergillus* and *Penicillium* genera have been and continue to be well studied, there still exists opportunites for the discovery of novel bioactive metabolites and natural products from isolates within these taxanomic groups.

While the majority of the endophytes fell within the ascomycota division, the largest division within the fungi kingdom, eight endophytes were identified within the basidiomycota division. Three of these endophytes were identified at the species level as *Cryptococcus flavescens* and *Trametes versicolor* (2). *Trametes versicolor* is a mushroom, commonly referred to as the turkey tail mushroom, that grows on dead hardwood across North America. With a vast history in ancient Chinese medicine, *Trametes versicolor* has since been shown to produce a number of bioactive metabolites including polysaccharides that exhibit antioxidant activity,[75,76] and proteins such as TVC that act as immunostimulants.[77] Additionally, *Trametes versicolor* has been known for producing products that show anti-tumor properties[76,77] and was recently shown potential to aid in blood sugar regulation and prevention of diabetic complications.[78] In addition to what is known about *Trametes versicolor*, *Cryptococcus flavescens* has been reported as a biocontrol agent for Fusarium head blight (FSH), a fungal disease that affects cereal crops and impacts kernel development.[79,80] Despite being widely known as a biocontrol agent, *Cryptococcus flavescens* has also been shown to produce xylanase, an enzyme that plays a role in both digestion and human health.[81]

The examples highlighted above illustrate that the endophytes within the NPRG library represent a diverse collection of fungi that possess the ability to produce natural products and bioactive metabolites that can serve in several applications. In obtaining an identification for these endophytes, researchers have the ability to target potential projects and isolation efforts to

obtain potentially new natural products or study a relatively unknown endophyte for further discovery.

Application Potential

With the constant need to discover natural products, researchers are often faced with the frustrating task of prioritizing projects that could lead to the isolation of natural products with known properties and applications, or projects that have the potential to lead to novel products that have not been previously isolated or identified. In this regard, DNA taxonomy as a tool that leads to an unambiguous identification of fungal isolates is important as it allows both targeted isolation efforts of a specific natural product and the selection of a project based on the possibility of isolating a new natural product. Given that the production of natural products is often species specific, the ability to identify isolates to a high taxonomic level allows researchers attempting to re-isolate a particular natural product to target isolates with the desired biosynthetic potential. Alternatively, if an isolate is identified as a species that has not been extensively researched, the project could be prioritized to increase the likelihood of isolating novel natural products. This second concept could be extended to investigating the natural products produced by isolates within related genera, families and orders as a means of determining which group of isolates should or could be focused on. In this way DNA taxonomy provides a valuable and efficient first step in the prioritization methods used by natural products researchers.

Conclusion

Identification has been a limitation that has surpassed endophytes alone, with numerous accounts of improper identifications being found in all domains of life from flora to fauna alike.[82-84] Put simply, misidentifications, especially at the species level, occur easily and can be

attributed to several factors, from misleading characteristics to convergent evolution. One of the main causes of misidentification is that an identification that is based on a taxonomic approach often does not match data that is retrieved when conducting a molecular identification. As such, it has been strongly recommended that whenever possible the identification of an unknown organism be obtained by molecular methodology in combination with morphology or an alternate traditional approach based on the visual characteristics of an unknown.[26] The research described in this thesis, though only completed on a single library of isolates, has shown promising results that support the recommendation of utilizing molecular methods to obtain an identification on an unknown organism and has laid the foundation for the unambiguous identification of fungal endophytes by the NPRG in the future.

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Appendix 1 DNA Sequences

CT1-005A

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JAJ1-097

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JAJ1-113

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JAJ1-117

Primer: ITS1

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JAJ1-129

Primer: ITS1

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JAJ1-133

Primer: ITS1

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JAJ1-137

Primer: ITS1

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JAJ1-141

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JAJ1-157

Primer: ITS1

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JAJ1-161

Primer: ITS1

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KP1-017A

474 bp

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KP1-017C

608 bp

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KP1-017E

509 bp

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KP1-045C

469 bp

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KP1-045K

475 bp

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KP1-063J

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KP1-063N

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KP1-075B

469 bp

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KP1-089A

481 bp

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KP1-119C

519 bp

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KP1-119E

489 bp

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KP1-123A

422 bp

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KP1-131BB

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KP1-131C

471 bp

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KP1-131DA

468 bp

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KP1-131DB

507 bp

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KP1-131F

494 bp

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KP1-131H

488 bp

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KP1-131J

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KP1-131K

482 bp

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KP1-131N

523 bp

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KP1-131Q

513 bp

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KP1-131R

497 bp

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KP1-131S

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KP1-131T

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KP1-131V

387 bp

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KP1-131Y

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KP1-131Z

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KP1-135C

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KP1-135D

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KP1-143A

275 bp

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KP1-143D

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tatc

KP1-175G

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KP1-175L

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KP2-001C

515 bp

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KP2-001F

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KP2-009A

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KP2-013F

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KP2033E

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Appendix 2 Maximum Likelihood example

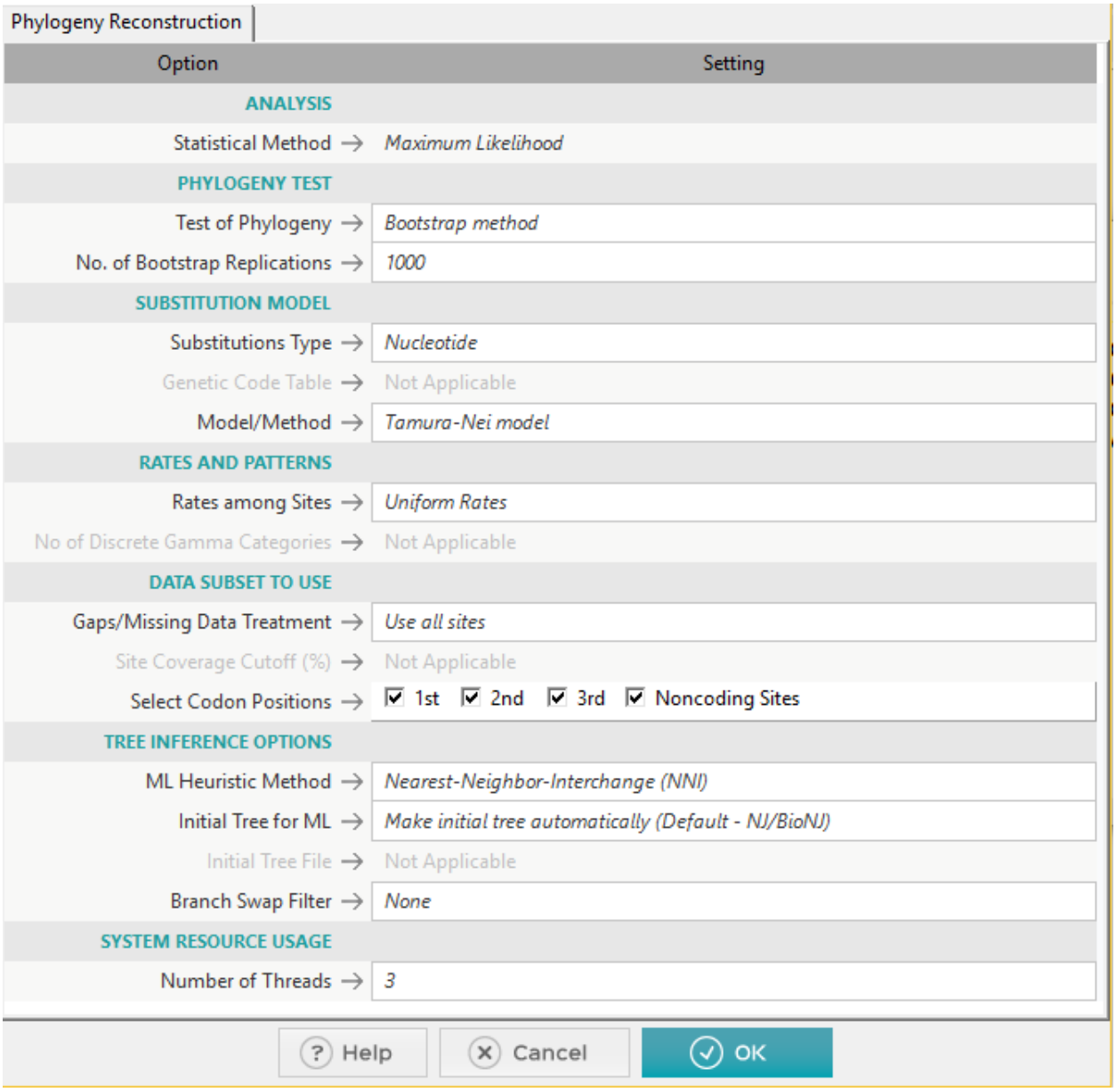

Figure 6: MEGA version X maximum-likelihood tree building parameters

Appendix 3 Phylogenetic tree output

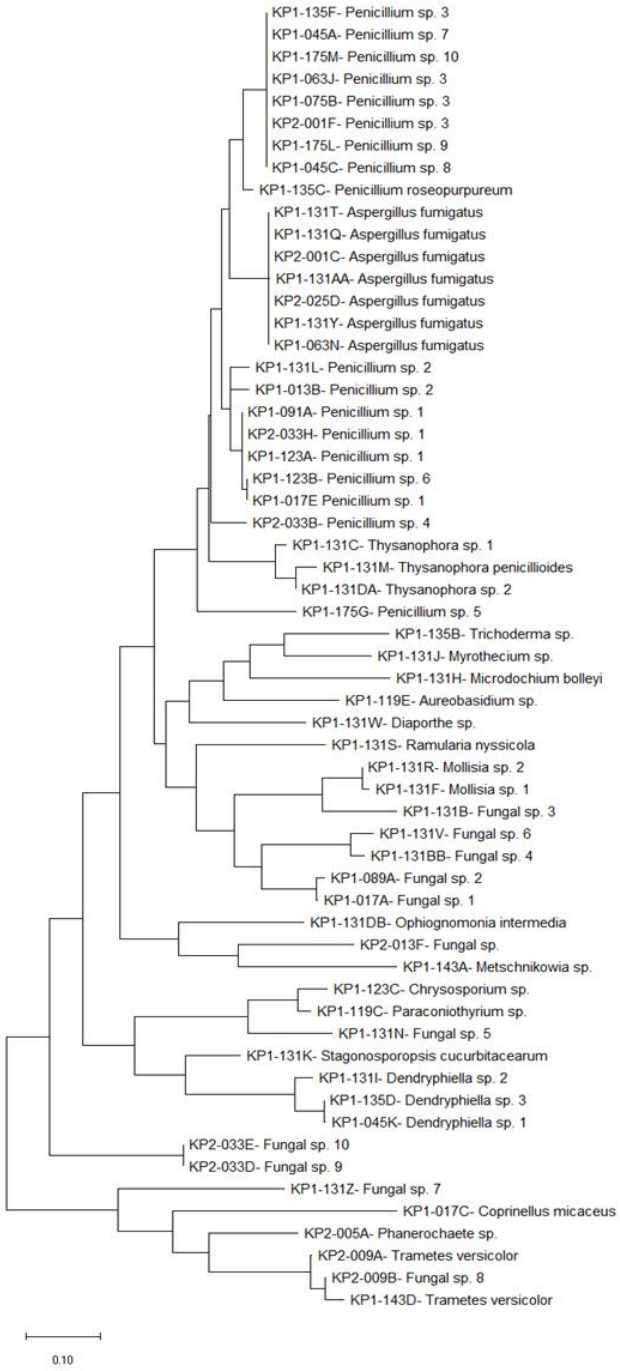

Figure 7: KP Isolate tree from MEGA version X phylogeny analyses

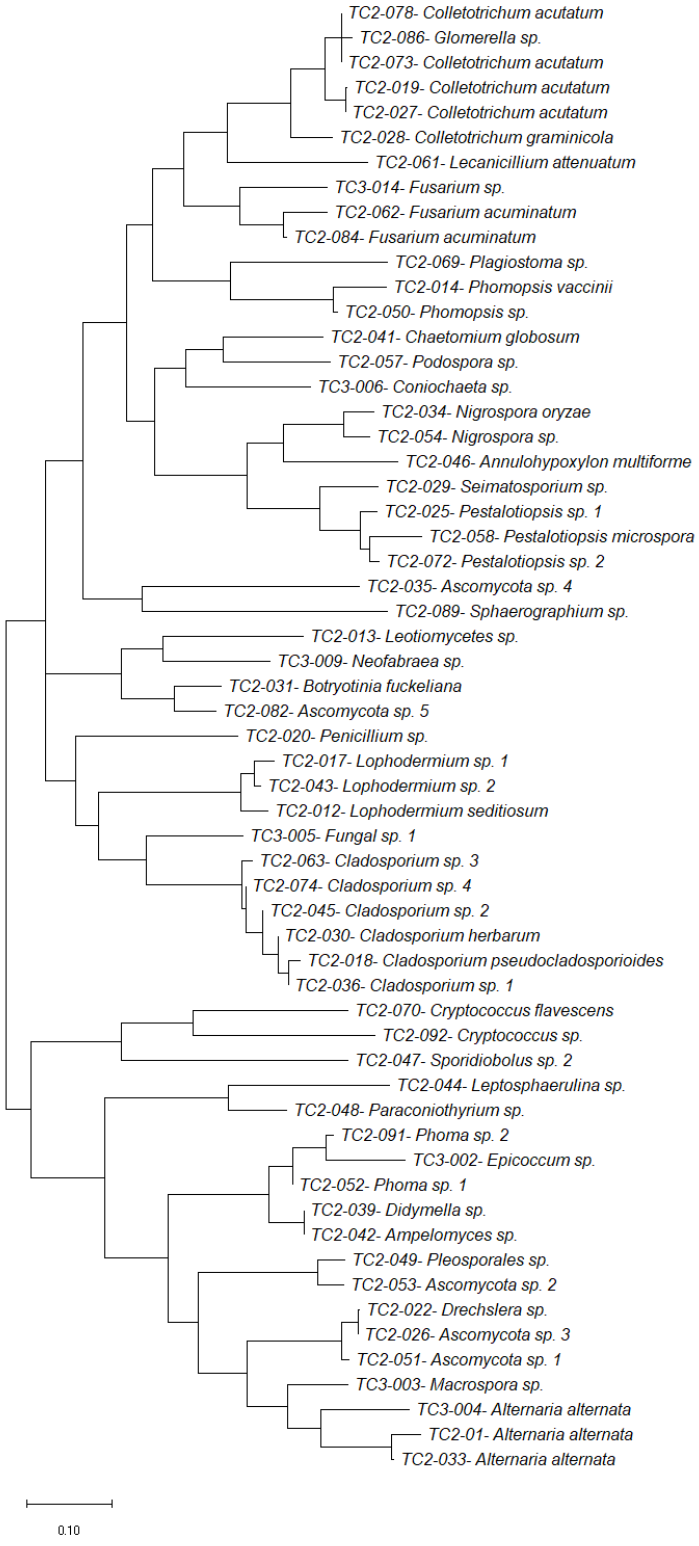

Figure 8: TC Isolate tree from MEGA verion X phylogeny analyses

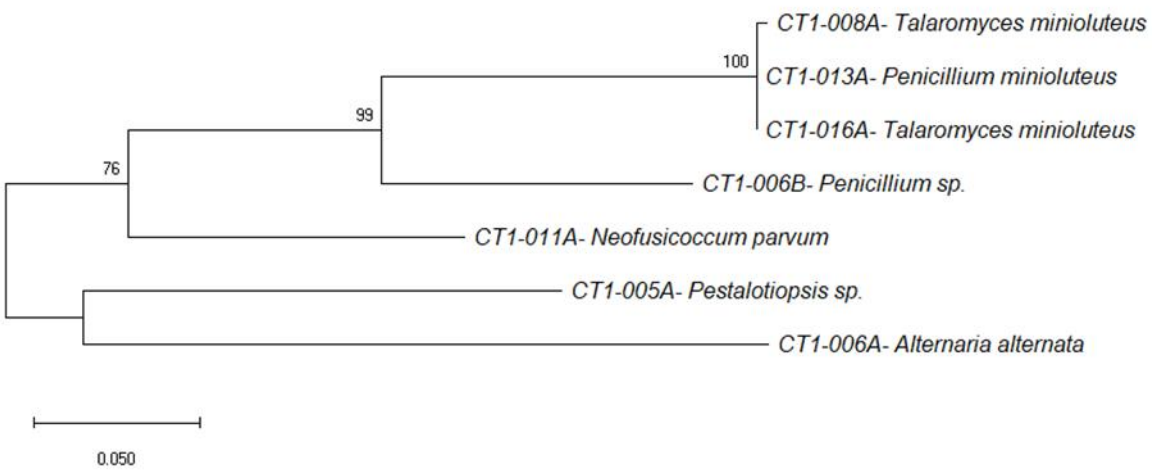

Figure 9: CT1 Isolate tree from MEGA version X phylogenetic analyses

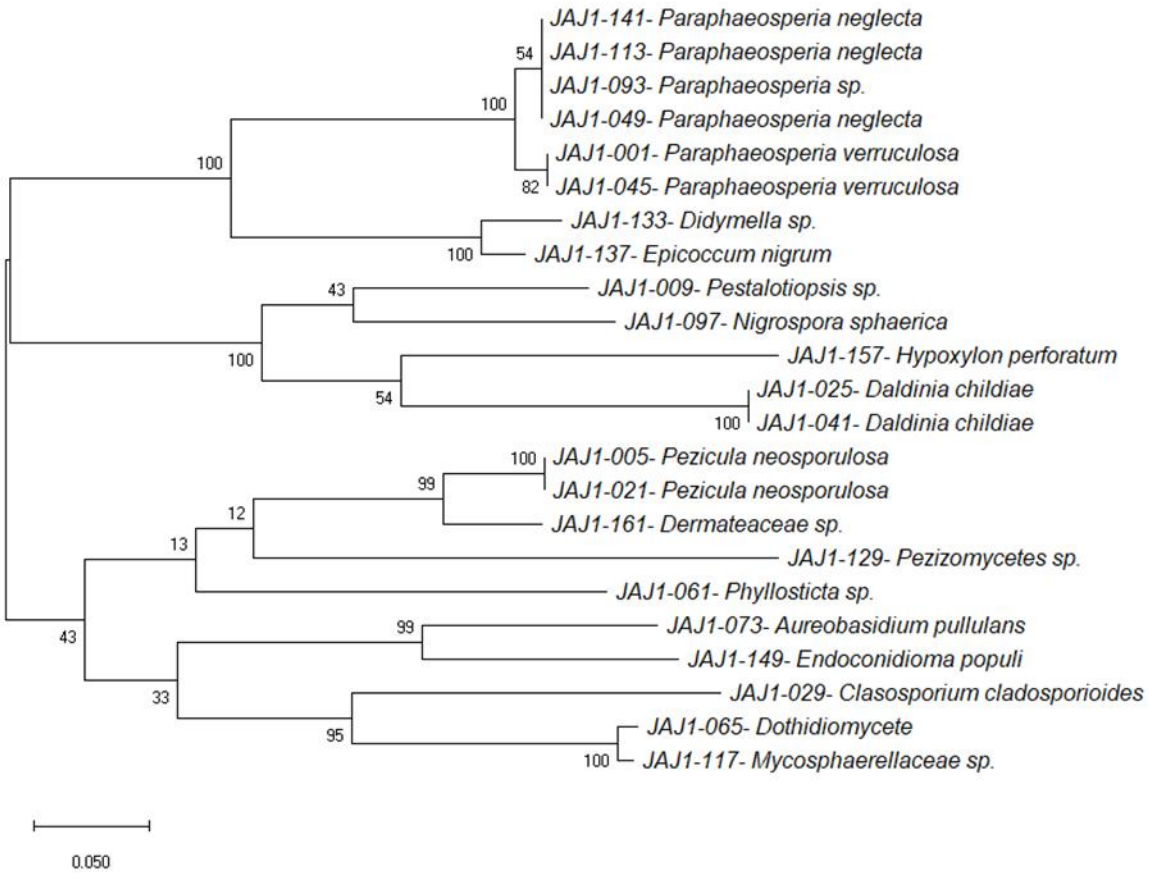

Figure 10: JAJ1 Isolate tree from MEGA version X phylogeny analyses