

# Molecular analysis reveals a distinctive fungal endophyte community associated with foliage of montane oaks in southeastern Arizona

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## Abstract

Sudden oak death (SOD), an emerging disease caused by the introduced oomycete *Phytophthora ramorum*, poses a serious threat to oak woodlands in the western US. Previous research has shown that foliar endophytes – fungi that live within apparently healthy leaves of plants without causing disease – can be effective as biological control agents in protecting trees against *Phytophthora* infection. Here, we examine the endophyte communities associated with foliage of with seven oak taxa (*Quercus arizonica*, *Q. emoryi*, *Q. gambelii*, *Q. grisea*, *Q. hypoleucooides*, *Q. rugosa*, and *Q. arizonica* X *Q. rugosa*) in the Santa Rita Mountains in southeastern Arizona. In addition to providing a first description of the diverse community of endophytes associated with foliage of healthy oaks, we compare this community with endophytes found in three other tree species in southern Arizona (*Pinus ponderosa*, *Cupressus arizonica*, and *Platycladus orientalis*). We show that (1) oaks in southeastern Arizona harbor endophytes that are characterized by high genotypic and phylogenetic diversity; (2) more closely related oaks do not necessarily share more endophytes than do more distantly related oaks; and (3) relative to endophytes of other trees in the same biogeographic region, oak endophytes are distinctive at both the genotype level and in terms of the major lineages of fungi they represent. These fungi, archived as living vouchers at the Robert L. Gilbertson Mycological Herbarium, represent a first step toward identifying the very poorly known communities of endophytes associated with plants in Arizona, and will provide the raw material for bioassays assessing endophyte-mediated biological control of *Phytophthora* spp.

## Introduction

Sudden oak death (SOD) is an emerging disease that has destroyed over 4000 ha of coastal forest in California, Oregon, and Washington (Rizzo *et al.*, 2003). Since its inadvertent introduction, *Phytophthora ramorum*, the causal agent of SOD, has negatively affected the balance of forest ecosystems in a growing area of the western US. Tree loss and subsequent ecological shifts have led to an increased risk of fire, fundamental changes in plant community structure, and depreciation of local property values in affected communities (McPherson *et al.*, 2005; APHIS, 2005).

The oak woodlands of Arizona and Nevada are at risk for SOD due to the potential for transmission of infective propagules in nursery plants, via human travel, and through possible range expansion given the ability of *P. ramorum* to infect phylogenetically diverse plant species (Rizzo *et al.*, 2005). Susceptibility of oaks to SOD in western woodlands varies among conspecific individuals within a given geographic area (Rizzo *et al.*, 2005), suggesting that characteristics of individual trees or microhabitats influence infection success. Several research groups are examining the effects of microclimate and genotypic differences among individuals that may shape susceptibility to this invasive pathogen.

In addition to these factors, it is likely that the fungal community associated with trees may limit infection by *P. ramorum*. Specifically, fungal endophytes (fungi inhabiting asymptomatic tissues of living plants) occur in foliage and woody tissues of all major lineages of land plants, including species that dominate western US forests (e.g., Petrini & Carroll, 1981; Hoffman & Arnold, in revision). Previous work has shown that foliar endophytes can protect a focal angiosperm tree, *Theobroma cacao*, against a virulent strain of *Phytophthora* (Arnold *et al.*, 2003), suggesting that endophytes may be key biological control agents for *P. ramorum* in Arizona oaks. However, little is known regarding the diversity, species composition, or ecological roles of endophytic fungi inhabiting healthy oaks in Arizona.

Previous studies recovered three dominant species of fungi from foliage of *Quercus emoryi* in central Arizona (*Ophiognomia cryptica* sp., *Asteromella* sp., and *Plectrophomella* sp.; Faeth & Hammon, 1996). That work evaluated oviposition preferences of leafminers based on the infection

frequency of fungal endophytes in *Q. emoryi* leaves. Gaylord *et al.* (1996) found that endophyte community structure was affected by hybridization events between *Q. grisea* and *Q. gambelii*. That study also found correlations between frequency and composition of endophyte populations and unexplained mortality of a leaf-mining moth. Similarly, endophytes of *Q. garryana* in the Pacific Northwest protect plants against a cynipid gallformer (Wilson, 1995). To our knowledge, however, the majority of Arizona's oak species have not been surveyed for endophytic fungi, and the biological control potential of those fungi remains unknown.

Here, we present results of preliminary surveys of endophytic fungi associated with seven oak taxa representing the sections *Quercus* and *Lobatae* within the genus *Quercus*: *Q. arizonica*, *Q. emoryi*, *Q. gambelii*, *Q. grisea*, *Q. hypoleucoides*, *Q. rugosa*, and a hybrid oak (*Q. arizonica* X *Q. rugosa*) in the Santa Rita Mountains in southeastern Arizona. In addition to providing a first description of the diverse community of endophytic fungi associated with foliage of healthy oaks, we compare this community with endophytes found in three other tree species in southern Arizona (*Pinus ponderosa*, *Cupressus arizonica*, and the non-native ornamental, *Platycladus orientalis*). We show that (1) oaks in southeastern Arizona harbor diverse endophytes that are characterized by high genotypic and phylogenetic diversity; (2) more closely related oaks do not necessarily share more endophytes than do more distantly related oaks; and (3) relative to endophytes of other trees in the same biogeographic region, oak endophytes are distinctive in terms of the genotypes and the major lineages of fungi they represent.

## **Materials and Methods**

*Field collections and endophyte isolations.* We collected apparently healthy, mature leaves of *Quercus* spp. during August and September 2006 from Madera Canyon (Santa Cruz County, 31.725°N, 110.8794°W; elevation 1497m), a riparian zone on the northwestern flank of the Santa Rita range. Focal hosts represented common species of oaks in southeastern Arizona, including members of section *Quercus* (white oaks: *Q. arizonica*, *Q. gambelii*, *Q. grisea*, *Q. rugosa*, and a hybrid representing *Q. arizonica* X *Q. rugosa*) and section *Lobatae* (*Q. emoryi* and *Q. hypoleucoides*). Three

leaves from each of three individuals per species were rinsed in running tap water for 30 seconds and then cut into 2 mm pieces prior to surface sterilization. Sixteen pieces per leaf were agitated in 95% ethanol for 30 sec, 10% bleach solution (0.5% NaOCl) for 2 min, and 70% ethanol for 2 min, allowed to surface-dry under sterile conditions, and then plated on 2% malt extract agar (MEA) (Arnold *et al.*, 2007). To confirm the quality of surface sterilization, a subset of tissue pieces was pressed against the medium under sterile conditions for 30 s, and then removed. No mycelial growth was observed from these surface impressions.

Hyphal growth from the interior of leaf pieces was monitored for eight weeks. Using aseptic technique, emergent fungi were transferred to axenic culture on 2% MEA in 60 mm Petri plates prior to DNA extraction (see below). Mycelial samples were archived as living vouchers in sterile water at the Robert L. Gilbertson Mycological Herbarium at the University of Arizona (ARIZ).

*Additional host sampling.* To our knowledge, no published datasets exist regarding the endophytes of trees in southeastern Arizona. Therefore, to provide a preliminary assessment of the specificity of endophytic fungi associated with oaks, we examined endophyte communities associated with three additional tree species in Pima and Santa Cruz counties: *Pinus ponderosa* (Pinaceae), *Cupressus arizonica* (Cupressaceae), and *Platyclusus orientalis* (an introduced ornamental; Cupressaceae). Endophyte isolation and vouchering followed the methods described above. Individuals of *Pi. ponderosa* were sampled in the Santa Catalina Mountains (Bear Canyon, Pima County; 32.374°N, 110.690°W, elevation 1600m). *Cupressus arizonica* and *Pl. orientalis* were sampled at the University of Arizona Campus Arboretum in Tucson (32.231°N, 110.952°W, elevation 787m). Previous studies have indicated that endophyte communities differ among major biogeographic provinces (Arnold & Lutzoni, 2007; Hoffman & Arnold, in revision), but that temperate-zone endophyte communities do not differ markedly over the relatively small elevational and intersite differences in our study (Arnold *et al.*, 2007). Comparisons of oak endophytes against those of conifers from the same biogeographic region thus provides a first estimate of the potential for particular endophytes to infect these distantly related plants.

*DNA extraction and PCR.* Because the majority of endophytes did not sporulate in culture, we were unable to identify isolates beyond the level of phylum using morphology alone. For that reason, total genomic DNA was extracted directly from pure cultures following Arnold *et al.* (2007). The polymerase chain reaction (PCR) was used to amplify the nuclear ribosomal internal transcribed spacers and 5.8s gene (ITS, ca. 600 bp). Primers included ITS1F or ITS5 and ITS4 (White *et al.*, 1990). Sigma Readymix™ REDTaq™ was used for all PCR reactions. The 25µl reaction mixture included 12.5 µl of REDTaq™, 1 µl of each primer (10 µM), 1 µl of DNA template, and 9.5 µl of PCR-quality water. Cycling reactions were run on an MJ Research PTC200™ thermocycler as follows: 94°C for 3 minutes; 36 cycles of 94°C for 30 seconds, 54°C for 30 seconds, 72°C for 1 minute; and 72°C for 10 minutes. SYBR® Green I stain was used to detect DNA bands on a 1% agarose gel. All products demonstrated single bands.

*Sequencing and analyses.* PCR products were cleaned, quantified, and normalized at the GATC sequencing facility at the University of Arizona. Bidirectional sequencing was performed on an Applied Biosystems 3730XL DNA Analyzer. The software applications phred and phrap (Ewing & Green, 1998; Ewing *et al.*, 1998) were used to call bases and assemble contigs, with automation provided by the ChromaSeq package (D. Maddison & W. Maddison, 2005a) implemented in Mesquite v. 1.06 (W. Maddison & D. Maddison, 2005). All base calls were verified by inspection in Sequencher version 4.5 (Gene Codes Corp., Ann Arbor, MI.). Taxon-accumulation curves were generated in EstimateS (Colwell, 2004) using 50 randomizations of sample order.

Forty-four isolates from *Quercus* spp. in southeastern Arizona were compared against 163 representative isolates from *Pi. ponderosa*, *C. arizonica*, and *Pl. orientalis*. Initial comparisons were based on 99% ITS rDNA sequence similarity, which allowed us to assess the frequency with which particular genotypes of oak endophytes were recovered from other hosts while allowing for up to 1% sequencing error. Endophytes were identified to order and class based on comparisons of ITS sequences against a phylogenetically referenced database of over 3400 sequences from endophytic

fungi (Arnold & Lutzoni, 2007). Endophytes were identified to genus based on congruent results from comparisons with that database coupled with BLAST searches in GenBank (ncbi.nih.gov).

## Results

Among 197 isolates of endophytic fungi from healthy foliage of trees in southeastern Arizona, we recovered 56 distinct genotypes (Fisher's alpha = 26.10; Shannon index = 2.94, Simpson's index = 7.52). Thirty-five genotypes were recovered only once (singletons; 62.5%). All were filamentous Ascomycota, including representatives of five classes (Pezizomycetes, Eurotiomycetes, Sordariomycetes, Dothideomycetes, and Leotiomycetes; Fig. 1). The steep taxon-accumulation curve and disparity between estimated and observed richness suggests that many more endophytes remain to be recovered among these plants in southeastern Arizona (Fig. 2).

Ten distinct genotypes of endophytic fungi were recovered among 44 representative isolates from *Quercus* spp. (Fisher's alpha = 4.08, Shannon index = 1.58, Simpson's index = 3.15). Together, these genotypes represented six orders and three classes of Ascomycota: Diaporthales, Phyllachorales, and Xylariales (Sordariomycetes); Pleosporales and the dothideomycetous order containing the Mycosphaerellaceae (Dothideomycetes); and Pezizales (Pezizomycetes) (Fig. 1).

Three genotypes of oak endophytes were found only once (singletons; 30%): genotype AZ, corresponding to *Geopyxis* sp. from *Q. hypoleuroides*; AN, corresponding to *Xylaria* sp. from *Q. arizonica*; and AAA, corresponding to *Alternaria* sp. 1 from *Q. hypoleuroides* (Table 1). Among the seven genotypes recovered more than once, only one was recovered from a non-oak host: *Alternaria* sp. 2 from *Q. emoryi* (AV, JO10900) was also recovered from *Platycladus orientalis* in Tucson (isolate 9009a). The six remaining genotypes were found at least twice and were recovered only from oaks. Three of those genotypes were recovered from only one oak species: *Sporomia* sp. (AX) from *Q. grisea*, *Plicaria* sp. (AL) from *Q. hypoleuroides*, and *Discula* sp. (AK) represented by six isolates from a hybrid oak (*Q. arizonica* X *Q. rugosa*). The remaining three genotypes were found in *Q. hypoleuroides* and *Q. arizonica* (AO; *Plectosphaera* sp. 2); *Q. hypoleuroides*, *Q. arizonica*, and *Q. rugosa* (AAB; a xylarialean species); and *Q. gambelii* and *Q. arizonica* (AM; *Cladosporium* sp.). The bootstrap estimate of total richness falls within the 95% confidence interval around observed

richness, indicating that we recovered a large proportion of the endophyte diversity present in southern Arizona oaks (Fig. 2B).

Endophytes present in oaks were similar in diversity to the community recovered from *Pi. ponderosa* (Fisher's alpha = 5.60). Seventeen distinct genotypes were recovered among 111 isolates; of these, 11 genotypes (64.7%) were recovered only once. Among six nonsingletons, all were recovered only from *Pi. ponderosa*. In turn, *Cupressus* harbored 11 genotypes among only 13 isolates; of these, nine genotypes were found only once (Fisher's alpha = 35.15). *Platyclusus* harbored 22 distinctive genotypes among 29 sequenced isolates; of these, 17 were singletons (Fisher's alpha = 41.73). Two nonsingleton genotypes were recovered from both *Cupressus* and *Platyclusus*, and one from *Platyclusus* was recovered from *Q. emoryi* (see above). All others were unique to their respective host species.

Endophyte communities associated with *Quercus* spp. were dominated by one genotype that accounted for 54.5% of isolates (a xylarialean species likely representing *Biscognauxia*; Xylariales, Sordariomycetes). Similarly, one species accounted for 58.6% of isolates from *Pi. ponderosa* (*Lophodermium* sp., Rhytismatales, Leotiomyces). Neither *Platyclusus* nor *Cupressus* harbored an endophyte community with a single dominant species. Overall, the Sordariomycetes were especially common among oak endophytes, but endophyte communities from other hosts were dominated by the Leotiomyces (*Pi. ponderosa*) or Dothideomycetes (*Cupressus*, *Platyclusus*) (Fig. 2).

## Discussion

Endophytes recovered from foliage of apparently healthy trees in southeastern Arizona represent a phylogenetically diverse array of Ascomycota, and comprise a large number of distinct genotypes. Overall, 35 of 56 genotypes (62.5%) were found only once, underscoring the high diversity of these microfungal communities. Similar frequencies of singletons have been observed in the highly diverse endophyte communities in Panama, where 50-70% of genotypes are typically found only once (Arnold *et al.*, in prep.).

Like the coniferous hosts examined here, oaks harbor distinctive endophyte communities. Among all genotypes recovered more than once, only 19% occurred in more than one plant genus. The majority of oak endophytes represented genotypes that were not recovered in other host plant taxa, highlighting the importance of screening oaks in Arizona for recovering distinctive fungal symbionts.

Our data suggest that the most common genotypes of oak endophytes (e.g., AAB, Xylariales) occur in multiple oak species. Given the sampling of multiple oak species, the diversity of endophytes in oaks was lower than that of the coniferous hosts examined here, likely reflecting the longer leaf lifetimes of hosts such as *Pinus*, *Cupressus*, and *Platycladus* (Arnold *et al.*, 2003).

In the present study, few endophytes were recovered from *Q. gambelii* and *Q. emoryi*, even though they have been shown to harbor numerous endophytes in previous studies in other sites (e.g., Faeth & Hammon, 1996; Gaylord *et al.*, 1996). Further study is warranted to explore the reasons for the low isolation frequencies observed among leaves of these species from Madera Canyon.

The distinctiveness of endophyte assemblages in each host was evident not only at the genotype level, but also at higher taxonomic levels. The dominance of the Sordariomycetes among oak endophytes, Leotiomycetes among pine endophytes, and Dothideomycetes among the endophytes of Cupressaceae is consistent with previous studies in other biogeographic regions (e.g., eastern semideciduous forest; Arnold *et al.*, 2007; Arnold & Lutzoni, 2007). The potential for these classes of Ascomycota to have diversified with their respective hosts remains to be evaluated.

More generally, assessing specificity of fungal communities requires broad geographic and taxonomic sampling, as well as sampling to the point of asymptotic taxon-accumulation curves. Some patterns suggested by our preliminary data – e.g., that more closely related oaks do not share more genotypes of endophytes than do more distantly related oaks – remain to be examined more rigorously pending the recovery of more nonsingleton genotypes. Future work should decouple spatial sampling from host sampling, providing a clearer assessment of the potential host specificity of endophytes in sympatric but distantly related hosts.



The fungal taxa recovered here represent an array of phylogenetically and ecologically distinct taxa. The dominant species found in oaks in other geographic regions (e.g., European woodlands) were not recovered here (cf. Gennaro *et al.*, 2003). We also did not recover the three genera of endophytes recorded previously in foliage of *Q. emoryi* near Superior, Arizona (Faeth & Hammon, 1996), indicating the need to sample focal hosts in different sites and plant communities. *Discula*, which we recovered from a hybrid oak (*Q. arizonica* X *Q. rugosa*), has been isolated previously from Oregon white oak, a member of the same subgeneric section (*Q. garryana*; Wilson & Carroll, 1994). Both *Discula* and *Alternaria* include pathogenic species, but also occur as endophytes in diverse host taxa (Kirk *et al.*, 2001; Arnold *et al.*, 2007). *Cladosporium*, *Biscogniauxia*, *Plicaria*, *Plectosphaera*, and *Geopyxis* are widespread taxa associated with living and dead plant material, and *Sporormia* is best known as a wood-infecting fungus (Kirk *et al.*, 2001). The genotypes of these genera recovered here, when compared against existing databases, suggested that our study has found previously unrecorded endophytic genotypes. The Xylariales, including *Xylaria*, are typically associated with wood rot, although many species are also endophytic – especially in tropical regions, possibly underscoring the Madrean distribution of many of our focal oaks. Several species have bioactive secondary metabolites (e.g., Jimenez *et al.*, in review). Only one species has been evaluated previously for biological control activity against *Phytophthora* sp., but no antipathogen activity was observed *in vivo* (Arnold *et al.*, 2003).

To our knowledge, none of the remaining genera isolated from oaks – or from any other host in this study – has been evaluated for biological control potential against *Phytophthora*. The living collection of endophytes archived from the present study provides a diverse library for bioassays assessing the potential for endophytes to inhibit *Phytophthora ramorum* in Arizona oaks, while the methods outlined here provide a set of approaches for further sampling of the highly diverse endophyte communities present in foliage of plants in southeastern Arizona.

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## Figure legends

**Fig. 1.** Relative abundance of classes of Ascomycota among endophytic fungi in healthy foliage of trees in southeastern Arizona: (A) entire dataset, and (B) host genera, arrayed by family.

**Fig. 2.** Genotype accumulation curves illustrating observed genotypic richness and estimated total richness (based on bootstrap estimates) of endophyte communities in healthy foliage of trees in southeastern Arizona: (A) entire dataset, and (B) endophytes of oaks.

**Table 1**

Isolate numbers, genotype groups based on 99% ITS sequence similarity, host taxa, and top BLAST matches for 197 endophytic fungi isolated in this study. BLAST matches are based on whole-sequence comparisons to GenBank records (Arnold & Lutzoni, 2007). BLAST results include top-matching accession numbers, taxonomic information where available, and an e-value indicating the probability of matching those top matches on the basis of chance alone.

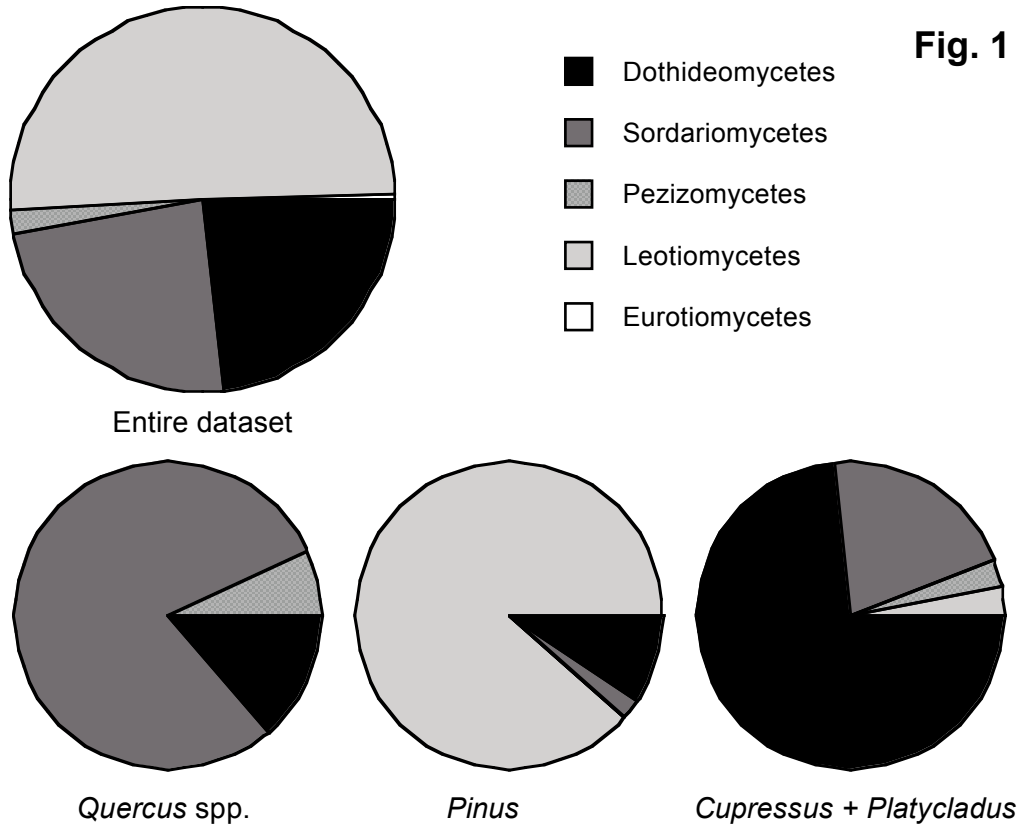
Isolate	Genotype	Host	Top BLAST match and e-value
JO10959	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10960	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10961	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10962	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10963	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10967	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10970	AN	<i>Quercus arizonica</i>	gb EF157664.1  <i>Xylaria</i> sp. NRRL 40192 0.0
JO10974	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10976	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10981	AAB	<i>Quercus arizonica</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10986	AO	<i>Quercus arizonica</i>	gb DQ923538.1  <i>Plectosphaera eucalypti</i> strain CBS 120063 0.0
JO10987	AO	<i>Quercus arizonica</i>	gb DQ923538.1  <i>Plectosphaera eucalypti</i> strain CBS 120063 0.0
JO10988	AM	<i>Quercus arizonica</i>	gb DQ008145.1  <i>Cladosporium cladosporioides</i> strain CBS 574.78 0.0
JO10900	AV	<i>Quercus emoryi</i>	gb AY154712.1  <i>Alternaria tenuissima</i> 0.0
JO10991	AM	<i>Quercus gambelii</i>	gb DQ008145.1  <i>Cladosporium cladosporioides</i> strain CBS 574.78 0.0
JO10895	AX	<i>Quercus grisea</i>	gb DQ384098.1  <i>Sporormia lignicola</i> strain CBS 363.69 00.
JO10902	AX	<i>Quercus grisea</i>	gb DQ384098.1  <i>Sporormia lignicola</i> strain CBS 363.69 0.0
JO10898	AO	<i>Quercus hypoleucoides</i>	gb DQ923538.1  <i>Plectosphaera eucalypti</i> strain CBS 120063 0.0
JO10899	AO	<i>Quercus hypoleucoides</i>	gb DQ923538.1  <i>Plectosphaera eucalypti</i> strain CBS 120063 0.0
JO10937	AZ	<i>Quercus hypoleucoides</i>	gb DQ220347.1  <i>Geopyxis carbonaria</i> 0.0
JO10938	AL	<i>Quercus hypoleucoides</i>	gb U38798.1  <i>Plicaria endocarpoides</i> (DAOM 195819) 5e-112
JO10947	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10949	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10950	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10952	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10953	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10954	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10965	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10966	AL	<i>Quercus hypoleucoides</i>	gb U38798.1  <i>Plicaria endocarpoides</i> (DAOM 195819) 5e-112
JO10969	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10973	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10979	AAA	<i>Quercus hypoleucoides</i>	gb AY154681.1  <i>Alternaria</i> sp. IA202 18S 0.0
JO10980	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10989	AAB	<i>Quercus hypoleucoides</i>	emb AJ390411.1  <i>Biscogniauxia atropunctata</i> 0.0
JO10993A	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10993B	AAB	<i>Quercus hypoleucoides</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10958	AAB	<i>Quercus rugosa</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10971	AAB	<i>Quercus rugosa</i>	gb DQ900943.1  Uncultured Xylariales clone 0.0
JO10896	AK	<i>Quercus</i> sp. (hybrid)	gb AF277139.1  <i>Discula quercina</i> 0.0
JO10897	AK	<i>Quercus</i> sp. (hybrid)	gb AF277139.1  <i>Discula quercina</i> 0.0
JO10903	AK	<i>Quercus</i> sp. (hybrid)	gb AF277139.1  <i>Discula quercina</i> 0.0
JO10904	AK	<i>Quercus</i> sp. (hybrid)	gb AF277139.1  <i>Discula quercina</i> 0.0

JO10905	AK	<i>Quercus</i> sp. (hybrid)	gb AF277139.1  <i>Discula quercina</i> 0.0
JO10992	AK	<i>Quercus</i> sp. (hybrid)	gb AF277139.1  <i>Discula quercina</i> 0.0
9295	AG	<i>Pinus ponderosa</i>	gb DQ239991.1  <i>Mycosphaerella irregulariramosa</i> voucher CMW 52 1e-14
9298	AG	<i>Pinus ponderosa</i>	gb AF297232.1  <i>Cercospora sorghi</i> f. <i>maydis</i> 5e-158
9302	AH	<i>Pinus ponderosa</i>	gb AF013228.1  <i>Hormonema dematioides</i> 0.0
9306	AG	<i>Pinus ponderosa</i>	gb AF309608.1  <i>Mycosphaerella irregulariramosa</i> clone 3e-147
9308	AG	<i>Pinus ponderosa</i>	gb AF297232.1  <i>Cercospora sorghi</i> f. <i>maydis</i> 2e-154
9310	V	<i>Pinus ponderosa</i>	emb AJ972795.1  <i>Monodictys</i> sp. MA 4647 0.0
9311	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 6e-167
9315	W	<i>Pinus ponderosa</i>	gb AF013222.2  <i>Cyclaneusma minus</i> 0.0
9317B	AG	<i>Pinus ponderosa</i>	gb AF309608.1  <i>Mycosphaerella irregulariramosa</i> 8e-154
9326	AG	<i>Pinus ponderosa</i>	gb AF297232.1  <i>Cercospora sorghi</i> f. <i>maydis</i> Kenya 5e-158
9329b	AG	<i>Pinus ponderosa</i>	gb AF309608.1  <i>Mycosphaerella irregulariramosa</i> 3e-147
9337	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 4e-162
9338A	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9338B	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9339	X	<i>Pinus ponderosa</i>	gb AY546004.1  Fungal endophyte WMS5 2e-83
9340	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 4e-162
9341	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 6e-167
9342	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 6e-167
9345	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9347	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 1e-165
9349	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9350	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9351	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9352	Y	<i>Pinus ponderosa</i>	gb AY971711.1  Fungal sp. 4.32 7e-173
9353	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9356	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 4e-162
9360	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9370A	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9370B	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9371	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9376	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9377	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9386	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9388	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9392	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9394	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9395	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9398	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9399	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9400	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9402	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9403	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9404	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9405A	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9405B	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9406	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9407	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9409	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9409	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9411	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9413	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9414	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9419	Z	<i>Pinus ponderosa</i>	gb AY971709.1  Fungal sp. 11.44 0.0
9421	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9423	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9424	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0

9425	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 2e-166
9426	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9426	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9428	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9430	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9436	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9437	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9438	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9440	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9441	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9442	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9443	AAD	<i>Pinus ponderosa</i>	gb AF433138.1  <i>Cudonia lutea</i> strain wz164 25S 0.0
9445	AA	<i>Pinus ponderosa</i>	gb AY969690.1  Uncultured ascomycete isolate dfmo0723_029 0.0
9446	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9449	AR	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9452	AH	<i>Pinus ponderosa</i>	gb AF013228.1  <i>Hormonema dematioides</i> 0.0
9453	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 4e-162
9461	AAD	<i>Pinus ponderosa</i>	gb AF433138.1  <i>Cudonia lutea</i> strain wz164 0.0
9465	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 6e-167
9467	AR	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9472	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9478	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9479	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9485	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9495	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9501	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9502	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9509	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9516	AJ	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9526A	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 1e-161
9530	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9532	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9533	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9540	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9568	AI	<i>Pinus ponderosa</i>	gb AY789297.1  <i>Heyderia abietis</i> strain HMAS71954 4e-162
9578	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9583	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9584	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9587	AR	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9609	AB	<i>Pinus ponderosa</i>	gb AY373892.1  <i>Emericella rugulosa</i> strain SRRRC 92 0.0
9616	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9626	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9627	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9630	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9632	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9639	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9646	AC	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9651	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9657	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9669	AD	<i>Pinus ponderosa</i>	gb AF260818.1 AF260818 <i>Mycosphaerella dearnessii</i> 0.0
9671	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9760	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9762	AAD	<i>Pinus ponderosa</i>	gb AY100656.1  <i>Lophodermium baculiferum</i> isolate mon2zem 0.0
9875	AE	<i>Pinus ponderosa</i>	gb AY700138.1  Fungal endophyte sp. CEY 19 0.0
9880a	AF	<i>Pinus ponderosa</i>	emb AJ888444.1  <i>Scedosporium prolificans</i> 4e-88
10764	A	<i>Cupressus arizonica</i>	gb AY780080.1  <i>Sordaria lappae</i> 0.0
10765	AP	<i>Cupressus arizonica</i>	gb AY293791.1  <i>Phoma herbarum</i> strain ATCC 12569 0.0
10767	AN	<i>Cupressus arizonica</i>	gb AY293791.1  <i>Phoma herbarum</i> strain ATCC 12569 0.0

10769	AN	<i>Cupressus arizonica</i>	gb AY293791.1  <i>Phoma herbarum</i> strain ATCC 12569 0.0
10770	AS	<i>Cupressus arizonica</i>	gb AY293791.1  <i>Phoma herbarum</i> strain ATCC 12569 0.0
9005	B	<i>Cupressus arizonica</i>	gb AY293791.1  <i>Phoma herbarum</i> strain ATCC 12569 0.0
9058	AU	<i>Cupressus arizonica</i>	gb AY546017.1  Fungal endophyte WMS23 0.0
9059	AU	<i>Cupressus arizonica</i>	gb AY546017.1  Fungal endophyte WMS23 0.0
9097	O	<i>Cupressus arizonica</i>	gi 12583572  <i>Thielavia subthermophila</i> 0.0
9104	P	<i>Cupressus arizonica</i>	gb AY510419.1  <i>Preussia similis</i> strain S19 0.0
9106	Q	<i>Cupressus arizonica</i>	gb AY465445.1  Dothideales sp. GS5N1b 0.0
9116	R	<i>Cupressus arizonica</i>	gi 66990744  <i>Monodictys</i> sp. MA 4647 0.0
9120	S	<i>Cupressus arizonica</i>	gb AY465445.1  Dothideales sp. GS5N1b 1e-159
9007	AP	<i>Platyclusus orientalis</i>	gb AY831558.1  <i>Leptosphaerulina trifolii</i> 0.0
9009a	AV	<i>Platyclusus orientalis</i>	gb AY154712.1  <i>Alternaria tenuissima</i> strain IA287 0.0
9015	C	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9021	D	<i>Platyclusus orientalis</i>	gb AY154712.1  <i>Alternaria tenuissima</i> strain IA287 0.0
9027	AP	<i>Platyclusus orientalis</i>	gb AY831558.1  <i>Leptosphaerulina trifolii</i> 0.0
9028	AW	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9030	AP	<i>Platyclusus orientalis</i>	gb AY831558.1  <i>Leptosphaerulina trifolii</i> 0.0
9031	AT	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9036	AT	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9038	E	<i>Platyclusus orientalis</i>	gi 30089120  <i>Chaetomium nigricolor</i> 0.0
9042	AW	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9051	F	<i>Platyclusus orientalis</i>	gb AY465446.1  Dothideales sp. GS2N1c 0.0
9054	AY	<i>Platyclusus orientalis</i>	gb AY183371.1  <i>Phoma glomerata</i> 0.0
9060	G	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9064	AS	<i>Platyclusus orientalis</i>	gb AY183371.1  <i>Phoma glomerata</i> 0.0
9065	AY	<i>Platyclusus orientalis</i>	gb AY183371.1  <i>Phoma glomerata</i> 0.0
9069	AQ	<i>Platyclusus orientalis</i>	gb AY219880.1  <i>Lecythophora</i> sp. UBCtra1453C 0.0
9079	AT	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9084a	H	<i>Platyclusus orientalis</i>	gb AF491556.1  <i>Peziza varia</i> KH-97-88 0.0
9084b	I	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9085	J	<i>Platyclusus orientalis</i>	gb AY213639.1  <i>Aureobasidium pullulans</i> 0.0
9089	K	<i>Platyclusus orientalis</i>	gb AF405301.1  <i>Bartalinia robillardoides</i> 0.0
9092	L	<i>Platyclusus orientalis</i>	gb AY198390.1  <i>Coniochaeta ligniaria</i> 0.0
9093	AQ	<i>Platyclusus orientalis</i>	gb AY219880.1  <i>Lecythophora</i> sp. UBCtra1453C 0.0
9094	M	<i>Platyclusus orientalis</i>	gb AY219880.1  <i>Lecythophora</i> sp. UBCtra1453C 0.0 0.0
9096	N	<i>Platyclusus orientalis</i>	gb AF182378.1  <i>Hormonema</i> sp. F-054 0.0
9149a	T	<i>Platyclusus orientalis</i>	gb AY561200.1  Foliar endophyte of <i>Picea glauca</i> 0.0
9149b	U	<i>Platyclusus orientalis</i>	gb AF312009.1  <i>Phyllosticta spinarum</i> 0.0
9157	AAC	<i>Platyclusus orientalis</i>	gb AF433138.1  <i>Cudonia lutea</i> strain wz164 0.0

**Fig. 1**





**Fig. 2**

