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Lost and found: the Bermudan *Donadinia seaveri* found in North America, with comments on its juniper associates

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ABSTRACT
Collections of a species referred to Sarcosomataceae (Pezizomycetes) from eastern North America were studied both morphologically and using nuc rDNA internal transcribed spacer (ITS) region (ITS1-5.8S-ITS2 = ITS) and approximately 800 bp from the 5′ region of the nuc 28S rDNA (28S) to construct a phylogeny. The analyses indicate that these collections are *Donadinia seaveri*, a species previously known only from Bermuda. Because the associated tree, *Juniperus bermudiana*, has declined as a result of insect attack, it was thought that *D. seaveri* might be extinct. This work indicates that it is not extinct but is present in eastern North America. The species is described, new distributional records are given, and its association with the genus *Juniperus* is discussed.

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Bermuda cedar; biogeography; Sarcosomataceae

INTRODUCTION

The species of *Donadinia* Bellem. & Mel.-Howell form a well-supported group within Sarcosomataceae as determined by Carbone et al. (2013). The genus is characterized as having dark brown to black stipitate apothecia and ellipsoidal, often ornamented ascospores with cyanophilic markings. These characters distinguish the genus from others in the family such as *Plectania* Fuckel, with smooth or wrinkled ascospores and lacking a stipe, and *Pseudoplectania* Fuckel, in which the species have globose ascospores. Carbone et al. (2011) reviewed the stipitate members of Sarcosomataceae then referred to the genus *Plectania*. Carbone et al. (2013) stated that many characters in the family intergrade morphologically and are of limited utility in defining genera. But genera can be distinguished through sequence analyses. One of the lineages defined by Carbone et al. (2013) included the stipitate species and was recognized as the genus *Donadinia*. There are five described species of *Donadinia* from around the Northern Hemisphere; an identification key is available (Carbone et al. 2014). In North America, only the snow bank fungus, *D. nigrella* (Seaver) M. Carbone, Agnello & P. Alvarado (= *Plectania nannfeldtii* Korf), was reported previously. In our studies of the Pezizales, several collections of a fungus agreeing in characters with those of *Donadinia* were found in eastern North America associated with *Juniperus virginiana*. We used them in molecular studies where they were listed as "*Donadinia* sp." (Harrington et al. 1999; Hansen and Pfister 2006; Perry et al. 2007; Pfister et al. 2008; Peric et al. 2013). These sequences are found in GenBank under the following accession numbers: AF104342, DQ220329, and DQ017593. In our initial studies, we realized that this taxon was close to *D. helvelloides* (Donadini, Berthet & Astier) Bellem. & Mel.-Howell, the type species of the genus *Donadinia*, but we were unconvinced of its distinction. With the summary work on the Sarcosomataceae by Carbone et al. (2013), it became apparent that our collections are not only congeneric with *Donadinia* but that they can be referred to *D. seaveri* (M. Carbone, Agnello & LaGreca) M. Carbone, Agnello & P. Alvarado.

When *Plectania seaveri* was described (Carbone et al. 2012) and later transferred to *Donadinia* (Carbone et al. 2013), the authors suggested that the species might be extinct because it had not been collected in Bermuda, the type locality, since the 1940s and was not reported from other regions. It is associated with *Juniperus bermudiana*, the endemic Bermuda cedar. This tree, long treasured for its durable wood and other products, had come under attack by the scale insects *Carulaspis minima* and *Lepidosaphes newsteadi*, which were accidentally introduced into Bermuda, probably in the 1940s (Adams 2014), where they caused the decline

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and death of native junipers. Perhaps because of an assumption that *D. seaveri* was host specific, it was considered likely that the species did not survive in the altered ecosystem of present-day Bermuda (Carbone et al. 2012). In this paper, we provide evidence for a broad distribution of *D. seaveri* that includes collections from the eastern USA.

To arrive at this finding, we produced sequences from an isotype of *Plectania seaveri* (identified as *Bulgaria melastoma* (Sowerby) Seaver by Seaver and Waterston [1946]) and compared it with our recently and previously obtained sequences from eastern USA.

MATERIALS AND METHODS

Specimens.—Six herbarium specimens of *Donadinia seaveri* were included in the DNA phylogenetic analyses. These are listed in "Specimens examined."

Molecular techniques and phylogenetic analyses.—In preparation for DNA extractions, tissues from herbarium samples were ground using a BIO 101 Thermo FastPrep FP120 Cell Disrupter (Qbiogene, Carlsbad, California). DNA extractions were performed using the Qiagen DNeasy Plant Mini Kit (Qiagen, Germantown, Maryland). Ground tissue was incubated in extraction buffer at 65 C for 1 h except for the oldest herbarium specimens, *Donadinia* FH 01142449 and FH 00458741, collected in 1922 and 1939, respectively. These were incubated for 5 h. DNA dilutions of 1/10 and 1/100 were used for polymerase chain reaction (PCR) amplification of the nuc rDNA internal transcribed spacer (ITS) region (ITS1-5.8S-ITS2 = ITS) and approximately 800 bp of the 5′ region of nuc 28S rDNA (28S). ITS was amplified using the primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). 28S was amplified using primers LROR and LR5 (Moncalvo et al. 2000). Two primers specific to *Donadinia* were designed to optimize PCR amplification of the oldest herbarium specimens, *Donadinia* FH 01142449 and FH 00458741. Primers were designed using *Donadinia* species sequences in conjunction with the National Center for Biotechnology Information (NCBI) Primer-BLAST tool (https://www.ncbi.nlm.nih.gov/tools/primer-blast/). The newly designed 5′ primer Donadinia18S.1783 (5′-CGCGAGTATGACAACTGTTCCG-3′) was used in combination with ITS4 to amplify the ITS, and the newly designed 5′ primer Donadinia28S.1922 (5′-TCTGGTGCCTTTGGGTGC-3′) in combination with LR5 was used to amplify the 28S gene.

All PCR reactions were done in a Bio-Rad C-1000 thermocycler (Hercules, California). The ITS PCR reactions used IProof High-Fidelity Master Mix (Bio-Rad). The thermal cycling protocol was as follows: initial denaturation at 98 C for 3 min, denaturation at 98 C for 5 s, annealing at 53 C for 30 s, and extension at 72 C for 5 min, with a repeat from the denaturation step 35 times and a final extension at 72 C for 5 min.

PCR products were purified using Qiagen's PCR Purification kit (Qiagen). Cycle sequencing, using BigDye 3.1 terminator (Applied Biosystems, Foster City, California), was done on the Bio-Rad C-1000 thermocycler using the following program: 96 C for 3 min, then 25 cycles of 96 C for 10 s, ramping 1.0 C/s to 60 C for 4 min, followed by a 4 C soak.

Sequencher 5.1 (GeneCodes, Ann Arbor, Michigan) was used to edit the DNA sequences. The ITS and 28S sequences were deposited in GenBank and are listed in TABLE 1, along with our isolates.

Table 1. Specimens included in phylogenetic analyses.

Taxon	Voucher	GenBank accessions ITS	28S
Scutellinia scutellata	OSC 100015	DQ491492	DQ247806
Pseudosarcosoma latahense	TUR-A 195801	JX669819	JX669856
Chorioactis geaster	FH ZZ2	AY307935	AY307943
Neournula pouchetii	TUR-A 195798	JX669837	JX669875
Trichaleurina celebica	TUR-A 195800	JX669839	JX669876
Trichaleurina javanica	TUR-A 195799	JX669838	JX669861
Pseudoplectania ericae	TUR-A 195790	JX669823	JX669863
Pseudoplectania melaena	MCVE 27433	JX669806	JX669842
Pseudoplectania nigrella	KL BK-4914	JX669807	JX669843
Sarcosoma globosum	KH.07.04	FJ499393	FJ499393
Galiella rufa	CBS 762.85	AF485072	KC012674
Urnula campylospora	PDD 83522	JX669830	JX669869
Urnula craterium	TUR-A 195794	JX669820	JX669857
Urnula hiemalis	TUR 196076	JX669828	JX669868
Urnula mediterranea	TUR-A 195796	JX669808	JX669844
Urnula padeniana	WTU-F-33051	JX669825	JX669866
Plectania megalocrater	TUR-A 195803	JX669809	JX669845
Plectania melastoma	TUR-A 195784	JX669814	JX669850
Plectania milleri	TUR-A 190823	JX669812	JX669848
Plectania rhytidia	TUR-A 195786	JX669813	JX669849
Plectania zugazae	AVM1467	JX669817	JX669854
Donadinia helvelloides 1	LY PB 940	JX669834	JX669872
Donadinia helvelloides 2	MCVE 28377	KP204907	KP204914
Donadinia lusitanica 1	MCVE 28378	KP204906	KP204913
Donadinia lusitanica 2	TUR-A 195792	JX669810	JX669846
Donadinia lusitanica 3	TUR-A 195791	JX669811	JX669847
Donadinia nigrella 1	WTU-F-017150	KP204911	KP204918
Donadinia nigrella 2	WTU-F-017148	KP204912	KP204919
Donadinia nigrella 3	TUR-A 195793	JX669836	JX669836
Donadinia sibirica 1	MCVE 28376	KP204909	KP204916
Donadinia sibirica 2	MCVE28374	KP204910	KP204917
Donadinia sibirica 3	MCVE 28375	KP204908	KP204915
Donadinia seaveri Bermuda**	FH 01142449	*KY794717	*KY794712
Donadinia seaveri NC	FH 00458740	*KY794718	*KY794713
Donadinia seaveri NC	FH 00458741	*KY794719	*KY794714
Donadinia seaveri MA	FH 00458441	*KY794720	*KY794715
Donadinia seaveri ME	FH 00458739	*KY794721	*KY794716
Donadinia seaveri NY	FH 00465512	*KY794722	DQ220329

Note. * indicates sequences obtained in this study, and **indicates the isotype of *Donadinia seaveri*. FH denotes Farlow Herbarium, Harvard University Herbaria, Cambridge, Massachusetts.

DNA sequence alignment.—Alignments of DNA sequences were done using Clustal W (1.82) through the CIPRES Science Gateway (ML; Miller et al. 2010) and then manually adjusted in Se-Al 2.0a11 (Rambaut 2002). The ITS and 28S sequences of the *Donadinia* isolates were aligned with GenBank sequences of select *Donadinia* species and other Sarcosomataceae, as listed in TABLE 1. The alignment was deposited in TreeBASE (study number S21089). The intra- and interspecific genetic distance of the *D. seaveri* specimens from ITS alignments was calculated using PAUP 4.0b10 (Swofford 2002).

Phylogenetic analyses of the ITS and 28S alignments used maximum parsimony (MP), PAUP 4.0b10 (Swofford 2002), and maximum likelihood (ML) with the GTRGAMMA model of rate heterogeneity and run on RAxML-HPC2 through the CIPRES Science Gateway (Miller et al. 2010). Branch support for MP and ML analyses was determined by 1000 bootstrap replicates. Posterior probabilities (PPs) were determined from a Markov chain Monte Carlo (MCMC) coalescent approach implemented in BEAST 1.8.2 (Drummond and Rambaut 2007), with a random local clock model allowing a certain amount of variation in clock rate across the tree. A GMRF Bayesian Skyride coalescent tree prior was used in all simulations with the general time-reversible model of nucleotide substitution + gamma + invariant sites (GTR+G+I) with a randomly generated starting tree. Four independent runs were done. Chains were run for 20 million generations, with sampling of parameters every 2000 generations. Tracer 1.6.0 (Drummond and Rambaut 2007) was used to check the effective sample size (ESS); burn-in values were adjusted to achieve an overall ESS of ≥200. A consensus tree with 0% burn-in value was generated using TreeAnnotator 1.8.2 and visualized in FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/). The PP, MP, and ML support values are displayed on the ML tree presented in FIG. 1. The outgroup taxon was *Scutellinia scutellata*.

RESULTS

In this study, ITS and 28S sequences were successfully obtained for an isotype of *D. seaveri* collected in 1922 in Bermuda (TABLE 1). ITS and 28S sequences also were obtained from collections of *Donadinia* species examined from eastern North America and associated with *Juniperus virginiana* (TABLE 1).

The ITS-28S rDNA sequence data set consisted of 1356 characters, of which 349 were parsimony-informative. Phylogenetic analyses of the ITS-28S sequence data sets determined that the five eastern North American *Donadinia* collections share an evolutionary lineage with *D. seaveri*. These results confirm that the five described species fall within the monophyletic genus *Donadinia*. The species included are *D. helvelloides, D. lusitanica* (Torrend & Boud.) M. Carbone, Agnello & P. Alvarado, *D. nigrella, D. seaveri*, and *D. sibirica* M. Carbone, Agnello, P. Alvarado & Krom.

The six specimens of *D. seaveri* form a highly supported clade (FIG. 1) within the monophyletic *Donadinia* and fall into two groups: isolates from the northeastern USA and isolates from Bermuda and North Carolina (FIG. 1). A comparison of *Donadinia* ITS sequences indicated there was 0.2–0.4% base pair difference among the northeast specimens and 0– 0.6% base pair difference among those from Bermuda/North Carolina (FIG. 1). Between these two groups of *D. seaveri*, up to 0.8% difference in ITS base pairs was determined. The *D. seaveri* clade is sister to the four other *Donadinia* species (FIG. 1). The minimal ITS sequence diversity observed supports the consideration that the six specimens of *D. seaveri* represent a single species that is not extinct but is represented by a broader geographic distribution than originally considered.

Among the specimens in the *D. seaveri* lineage, little intraspecific genetic diversity was found for the other *Donadinia* species: *D. helvelloides* (1.0%), *D. lusitanica* (0%), and *D. sibirica* (0.2%). The intraspecific diversity of ITS sequence for *D. nigrella* was greater than the other *Donadinia* species and ranged from 0% to 6.0%.

TAXONOMY

Donadinia seaveri (M. Carbone, Agnello & LaGreca) M. Carbone, Agnello & P. Alvarado, Ascomycete.org 5 (1):6. 2013 (2012). FIGS. 2, 3, 4

Typification: BERMUDA. Walsingham, on bark of *Juniperus bermudiana*, 20 Jan 1922, *H.H. Whetzel, Bermuda Fungi 188* (holotype: CUP, not seen; isotype: FH!)

Ascomata apothecial, gregarious to caespitose, with a short to long stipe, goblet-shaped to funnel-shaped, at maturity broadly expanded, margins upturned, often attached to the substrate with black binding hyphae. Hymenium dark brown, gray to black. Disc up to 1.5 cm wide, margin entire or split, sometimes wavy by mutual compression. Flesh about 300 µm thick. Outer surface black, tomentose, becoming wrinkled on drying. Texture leathery. Flesh from pale buff grading to black toward the outer surface. Asci up to 400 µm long, cylindrical, operculate, operculum sometimes slightly eccentric, J–, 8-spored, walls ca. 1 µm thick, tapering gradually

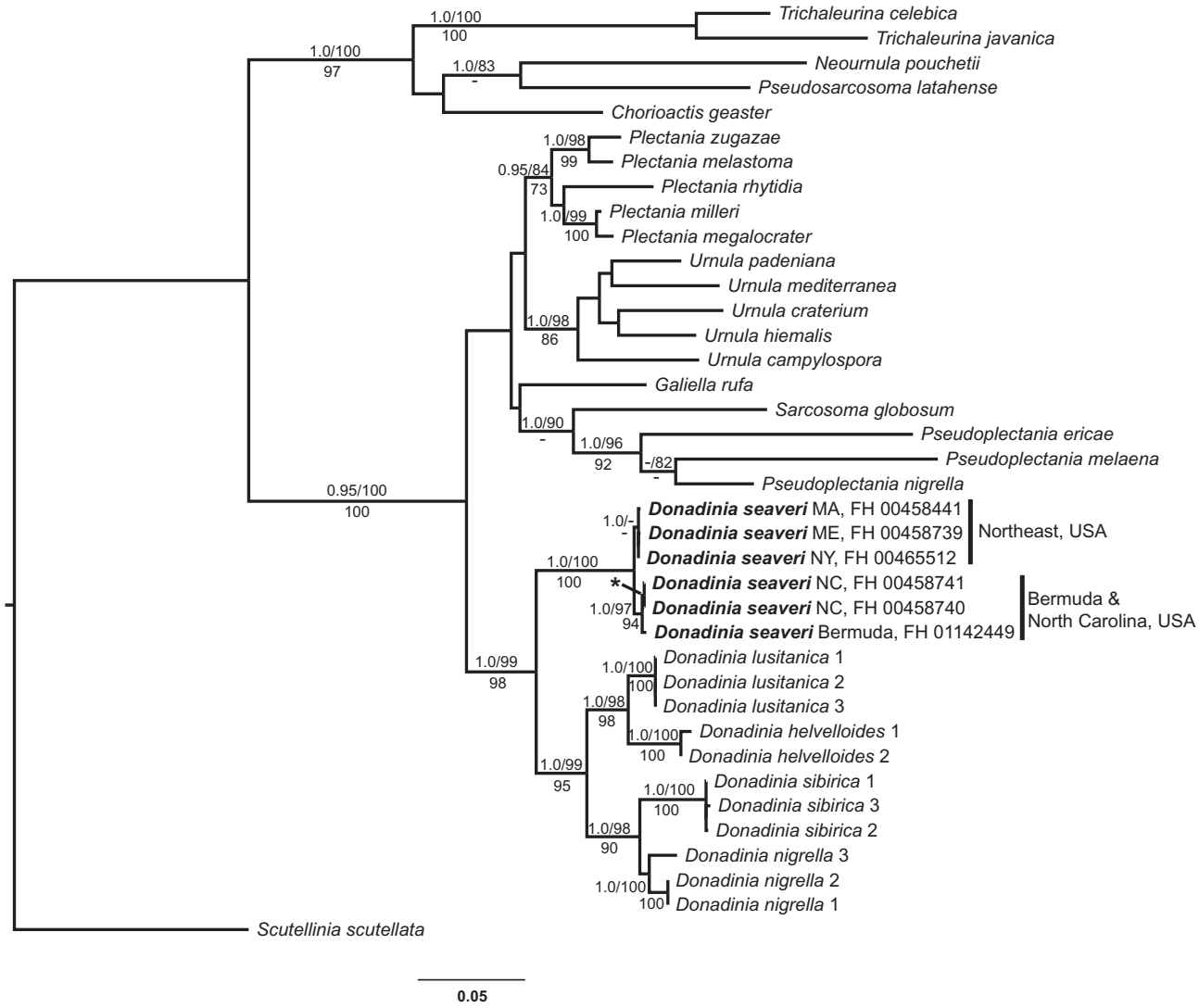

Figure 1. Maximum likelihood tree based on DNA sequence data from the nuc rDNA ITS region and the 28S gene. Posterior probabilities ≥0.95 and maximum likelihood (PP/ML) bootstrap values ≥70% are displayed above the branches. Maximum parsimony (MP) bootstrap values ≥70% are displayed below branches. The * on the branch leading to *D. seaveri* FH 00458741 and *D. seaveri* FH 00458740 (both from North Carolina, USA) represents a PP value of 1.0 and no MP and ML support. *D. seaveri* FH 01142449 is an isotype of *D. seaveri*. The outgroup taxon is *Scutellinia scutellata*.

toward the base, terminating with a simple septum. Paraphyses equal to the asci in length, 3–4 µm wide, septate, agglutinated, branched toward the apex, embedded in a matrix that includes brownish granules. Hymenial hairs (setae) present, cylindrical, slightly exceeding the hymenial layer, more or less cylindrical, walls brown, septate only toward the base. Ascospores ellipsoidal, 20–27 × 9.5–12 µm, hyaline, with many small oil droplets, walls 1 µm thick, ornamented with small, isolated, rounded warts less than 1 µm in height and width. Subhymenium of tightly woven textura intricata more or less amber. Medulla of textura intricata of hyphae 4–10 µm wide surround by dense gelatinous material, hyphae thick-walled up to 1 µm thick, dark in both the upper and lower regions but hyaline or yellowish centrally, outer excipulum of angular cells, cells up to 25 µm diam, walls highly pigmented and encrusted and generally indiscernible because of the accumulation of black material, outer cells giving rise to hyphal hairs that are cylindrical, septate, brown, long, smooth to finely encrusted with crystalline pigments. Basal hyphae 5–8 µm wide, septate, brown, more or less smooth.

Specimens examined: BERMUDA. Walsingham, on *Juniperus bermudiana*, 20 Jan 1922, *H.H. Whetzel, Bermuda Fungi 188* (isotype, FH 01142449). USA. MAINE: York Co., Ogunquit, Marginal Way Walk, base of juniper tree, 27 May 2013, *K. LoBuglio* (FH 00458739); MASSACHUSETTS: Middlesex Co., Weston, end of road

Figure 2. Apothecia of *D. seaveri* on debris of *J. virginiana* (left); at base of trunk (right). FH 00822407.

near Rt. 117, at base of trunk of *Juniperus virginiana*, 18 Apr 2004, *D.H. Pfister, K. Hansen 04-04, D. Hewitt, P. Inderbitzin* (FH 00458441); NEW YORK: Dutchess Co., Pleasant Valley, on dead twigs of *Juniperus virginiana* in secondary mixed forest, Apr 1996, *M. Potter mh669* and *M. Potter* (FH 00465512 and 00822407); as above, 29 Mar 1997, *F.A. Harrington mh682* (FH 00822409); NORTH CAROLINA: Durham Co., Catsburg, 36°2′57″N, 78°52′22″W, on dead juniper bark, 24 Feb 1939, *L.R. Hessler 12124* (TENN-F-012124; fragment FH 00458741); Wake Co., Raleigh, Possum Track Rd., Fishing Area, on *Juniperus virginiana*, 21 Mar 2003, *L.F. Grand & C.S. Vernia* (FH 00458740).

Comments: As suggested by Carbone et al. (2014), the verrucose ascospore ornamentation composed of rounded warts are more highly visible in this species than in others in the genus.

DISCUSSION

Species of *Juniperus* seem to be the common plant associate of all collections of *D. seaveri* we investigated. We therefore looked into the relationship among the new world species of *Juniperus*. In recent phylogenetic studies, *J. bermudiana* and *J. virginiana* are closely related taxa within the section Sabina clade III (Mao et al. 2010; Adams and Schwarzback 2013). *Juniperus virginiana* is widespread in eastern North America. Both plants involved, *J. bermudiana* and *J. virginiana*, are part of a clade that seems to have arisen from progenitors in the Appalachian region; they and the West Indian species all have floristic affinities with the eastern USA (Adams 1968).

Geologically, Bermuda was never connected to the mainland and possibly emerged in the Oligocene. The sand dune system, where *J. bermudiana* is found, developed <1 million years ago (mya) (Mao et al. 2010). We hypothesize that the ancestors of the juniper and *D. seaveri* arrived on Bermuda via dispersal from the North American continent. Diversification of the junipers may have been favored by the cooling and drying of the earth (Mao et al. 2010). Of some note then may be the observation that members of Sarcosomataceae are often able to withstand drying and/or conserve water in gelatinous tissues.

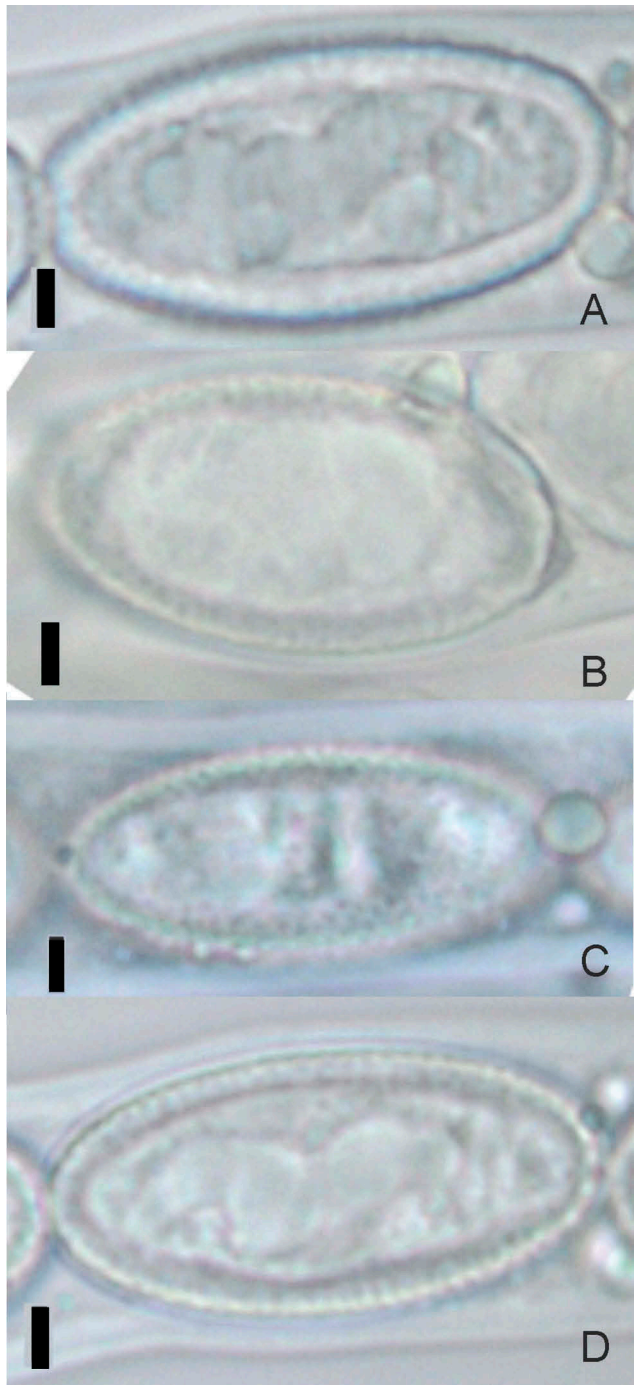

Figure 3. Ascospores of *D. seaveri*. A. FH 00458740. B. FH 00465512. C. FH 00458741. D. FH 00458741. Bars = 2 µm.

Figure 4. Hymenial details of *D. seaveri*. A. Section of hymenium with asci and immature ascospores and brown intertwined and encrusted paraphyses, Bar = 3 µm B. Septate paraphysis and seta with a basal septum. FH 00458441, Bar = 5 µm.

The habitat of *D. seaveri* as mentioned by Seaver and Waterston (1946:182) is important to note. They wrote that "this species [is] on rotten bark of *Juniperus bermudiana* L., from roots of living trees exposed at soil level…" Several of our collections were made at the bases of living trees and seemingly were connected with the trunk and roots of the tree. We do not know the biotic interactions that are involved with these fungi. We assume they are saprobic, but it is possible that they are endophytes or weak parasites. One of the locations for *D. seaveri* in the Boston, Massachusetts, area in the eastern USA was pinpointed by a local naturalist who referred us to a stand of mature *J. virginiana* that was in decline. In this particular area, many of the trees supported growth of *D. seaveri*.

The known species of *Donadinia* all are found in association with conifers. *Donadinia lusitanica* is primarily found with *Cupressus sempervirens* (Cupressaceae). *Donadinia helvelloides* is associated with *Taxus baccata* (Taxaceae). *Donadinia nigrella* is found with a variety of conifers in the western USA, mostly those in the Pinaceae, and *D. sibirica* is found with *Abies*, *Picea*, and *Pinus*, all members of the Pinaceae.

Our search for additional collections of *Donadinia* species in North America lead to two specimens from Quebec, Canada: (i) Moisie, Chalet, Saucier, 50.237164, −66.137079, Branche de sapin, dans un bois de sapins et d'epinettes noires [Fir branch, in a fir wood and black spruce], Jeanie Saucier (233), 21 May 2000 (CMMF004878); and (ii) Chicoutimi, 48.368277, −71.119642, sous conifère, relié à une branchette de conifère [under conifer, connected to a conifer branch], Gerard Guerin (377), 24 May 1985 (CMMF015592). These formed dark, stipitate apothecia and fruited in the spring in coniferous forests. They were identified as *Plectania nannfeldtii* (= *Donadinia nigrella*). Their ascospores are smooth under the light microscope and fall within the size range of *D. nigrella*. *Donadinia nigrella* is often collected in the western USA at the margins of melting snow banks but has not been reported in eastern regions of the continent. As was pointed out by Carbone et al. (2014) and confirmed in our study, the specimens so far sequenced of *D. nigrella* show considerable variation. We have not at this time sequenced the Canadian samples. It is likely that *D. nigrella* represents a species complex and these collections may represent additional outliers.

Although we may bemoan the loss of the Bermuda cedar in Bermuda, it is a species that has been moved around the world. It is invasive on the island of Saint Helena where it was introduced in 1859 (Adams 2014). At the same time, in Bermuda the gene stock is being diminished through interbreeding of *J. bermudiana* with *J. virginiana*, which is resistant to insect attack. Because of this resistance, *J. virginiana* was introduced when the native cedars were being decimated by the scale insect (Adams and Wingate 2008).

This example provides a cautionary note regarding assumptions of extinctions. Too often our knowledge of the distribution of fungi is extremely limited, and often the natural history, ecology, and interactions of fungi are inferred but not confirmed. It is only through detailed study that we can fully understand the status of particular lineages and their ranges.

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