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Monodictys arctica, a new hyphomycete from the roots of *Saxifraga oppositifolia* collected in the Canadian High Arctic

MELISSA J. DAY[1*], CONNIE FE C. GIBAS[1], KEI E. FUJIMURA[2], KEITH N. EGGER[2] & RANDOLPH S. CURRAH[1]

mjday@ualberta.ca

[1] *Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada*

[2] *Ecosystem Science and Management Program, University of Northern British Columbia, Prince George, BC, V2N 4Z9, Canada*

Abstract—*Monodictys arctica* sp. nov. is described on the basis of nine isolates obtained from the roots of eight separate collections of *Saxifraga oppositifolia* from Ellesmere Island, Nunavut, Canada. Conidia are multicelled, smooth, darkly pigmented, and globose, oblong, ellipsoidal, or pyriform to irregularly shaped or dichotomously branched, consisting of a blastically produced basal cell and a distal proliferation of up to 24 cells arising from meristematic growth. Analyses of SSU and ITS sequences indicate the species is unique but has an affinity to the loculoascomycete taxon *Leptosphaeria dryadophila*.

Key words —endophyte, DSE, taxonomy

Introduction

The surfaces and cortices of fine roots are usually heavily infected with darkly pigmented, septate hyphae, some of which are easily isolated after surface sterilisation and grow readily in culture (Addy et al. 2005). Among the more common and widely distributed species of these "dark septate endophytes" or "DSE" are the helotialean anamorphs *Phialocephala fortinii* C.J.K. Wang & H.E. Wilcox, *Leptodontidium orchidicola* Sigler & Currah, and *Scytalidium vaccinii* Dalpé et al.

A large collection of cultures, composed predominantly of "DSE" fungi, were isolated from the roots of *Cassiope tetragona, Dryas integrifolia, Salix arctica*, and *Saxifraga oppositifolia* collected during the summer of 2000 from Alexandra Fiord, Ellesmere Island, Nunavut, Canada (78° 53'N, 75° 55'W). The plants were collected as part of an experiment to study the effects of passive

*Author for correspondence

warming using open-topped chambers (OTCs) on root-associated fungal communities. Among this collection of fungi were numerous representatives of *P. fortinii*, *L. orchidicola*, and *S. vaccinii* along with isolates of other taxa. Eight of the latter, each from separate collections of *S. oppositifolia*, were distinctive in producing irregular, multicelled, darkly pigmented conidia that were assignable to *Monodictys* (anamorphic *Dothideales*, fide Kirk et al. 2001) but did not match any described species.

Here, we provide a description of *Monodictys arctica* along with a comparison of this new species with similar ones and, using sequence data from the small subunit and internal transcribed spacer regions on the ribosomal DNA, provide an estimation of its phylogenetic position among related taxa in the Loculoascomycetes (sensu Barr & Huhndorf 2001).

Materials and methods

Specimens of *Saxifraga oppositifolia*, from OTCs and ambient plots, were harvested along with surrounding soil, placed in Ziploc® bags, and stored at 4°C until processed at the University of Northern British Columbia. Soil was loosened from roots by immersing in water for at least 24 hours at 4°C. Roots were gently cleaned with water and then collected in a 0.5 mm sieve (No. 35 USA standard testing sieve, W.S. Tyler, Inc. Mentor, Ohio, USA). Randomly selected root sections were surface-sterilized with 30% H_2O_2 following Danielson (1984) and placed on modified Melin Norkrans (MMN) agar (Marx 1969) amended with streptomycin sulphate and chlortetracycline. Plates were incubated at room temperature (20–22°C) and isolates were purified by transfer to fresh media. A 0.5 mm plug from each isolate was placed on an MMN agar slant and stored at 4°C until it was sent to the University of Alberta for identification.

Colony characteristics of the new species were based on growth on oatmeal agar [OA; 20 g oatmeal, 20 g Select agar (Invitrogen, Carlsbad, California, USA), 1 L distilled water] and potato dextrose agar (PDA; Difco Bacto). Conidial morphology was examined using an Olympus BX50 microscope and slide cultures (Kane et al. 1997) mounted in polyvinyl alcohol with acid fuchsin [APVA; 1.66 g polyvinyl alcohol (Sigma Chemicals, Oakville, Ontario, Canada), 10.0 mL lactic acid, 1.0 mL glycerine, 10.0 mL H_2O, 0.02 g acid fuchsin] or 1.5 M KOH. Conidial and conidiophore dimensions are based on 140 and 20 measurements respectively and appear in the descriptions as a range. Images of conidia and colonies were prepared using an Olympus DP12 and an Olympus C60 camera, respectively. Freehand line drawings were made based on observations made with the light microscope.

To obtain the targeted rDNA sequences, cultures were grown on PDA overlaid with a Cellophane™ sheet (UCB Films, Bridgwater, Somerset, UK). Approximately 100 mg of mycelium was scraped off the cellophane and placed in a sterilised mortar containing acid-sterilised sand. Liquid nitrogen was added and the frozen mycelium was ground to a powder with a pestle. The powder was dissolved in 1 mL of 2x CTAB [10 mL 1M Tris pH 8.0, 8 mL 0.25M EDTA, 8.7 g NaCl, 20 mL 10% CTAB (10 g CTAB, 100 mL dH_2O), 100 mL dH_2O] and 2 µL β mercaptoethanol and incubated at 65°C for 2 hours. An equal volume of 24:1 chloroform:isoamyl alcohol was added. The tubes were inverted until an emulsion formed and then centrifuged for 20 min at 14 000 rpm at room temperature.

Table 1. Provenance data for species of *Leptosphaeria* and *Decorospora* used in the parsimony analysis of the ITS DNA region.

Species	Genbank Number	Host plant
Decorospora gaudefroyi	AF439451	Not listed
Leptosphaeria biglobosa	DQ133893	*Brassica napus*
L. conferta	AF439459	*Anacyclus radiatus*
L. doliolum	U04207	Not listed
L. dryadophila	AF439461	*Dryas octopetala*
L. maculans	M96384	*Brassica napus*
L. typharum	AF439465	*Typha angustifolia*
Monodictys arctica		*Saxifraga oppositifolia*

The upper DNA-containing layer was collected and purified using a Qiaquick PCR purifying kit (QIAgen Inc., Mississauga, Ontario, Canada). Cleaned extraction products were visualised on a 1% agarose gel stained with ethidium bromide and exposed to UV light.

The target DNA regions, the small subunit rDNA (SSU) and the internal transcribed (ITS) spacer region, consisting of complete ITS 1, 5.8 S, and ITS 2 and partial SSU and LSU DNA, were amplified using primers BMBCR (Lane et al. 1985) and NS8 (White et al. 1990) and BMBCR and ITS 4 (White et al. 1990) respectively. The PCR reaction mixture included 5 µL 10x buffer (500 mM KCl, 100 mM Tris Base pH 8.3), 26 µL distilled water, 3 µL 25 mM $MgCl_2$, 4 µL of dNTP (10 mM of each dNTP), 5 µL of each primer, 1 µL Taq DNA polymerase, and 1 µL of the DNA template. Amplifications were achieved in a GeneAmp PCR System 97000 (PE Applied Biosystems, Foster City, California, USA) with the following program parameters: 94°C for 2 minutes, 30 cycles of 94°C for 1 minute, 55°C for 1 minute, 72°C for 2 minutes, and an extension of 72°C for 7 minutes and 4°C for 10 minutes. Amplification products were subjected to electrophoresis on a 1% agarose gel stained with ethidium bromide and visualised under UV light.

The amplicons were purified using a QIAquick PCR purification kit (QIAgen Inc. Mississauga, Ontario, Canada) and both strands were sequenced using the primers BMBCR, ITS1 (White et al. 1990), ITS2 (White et al. 1990), and ITS4 (for the ITS region) and BMBCR, NS1, NS2, NS3, NS4, NS, NS5, NS6, NS7, and NS8 (White et al. 1990) for the SSU region. The sequencing reactions contained a DNA concentration of 50 nmol mL^{-1}, 0.5 µL primer, 2.5 µL sequencing buffer, 1 µL Big Dye v. 3.0 (Applied Biosystems Inc., Foster City, California, USA), and water up to a total of 10 µL. Cycle sequencing reactions were achieved using a GeneAmp PCR System 97000 (PE Applied Biosystems) with the following program parameters: 25 cycles of 94°C for 20 seconds, 50°C for 2 minutes, 60°C for 1 minute. Sequencing reactions were run on an AB 3100 Genetic Analyzer (Applied Biosystems Inc., Foster City, California, USA). Sequences were examined using Sequencher 4.0.5 (Gene Codes Corp., Ann Arbor, Michigan, USA). A BLAST search was performed in GenBank to find related sequences.

The SSU sequences were used to place the isolates within the Ascomycota. The ITS sequences were used to place the isolates within the genus to which they were most similar according to a BLAST search (Table 1). Sequences were manually aligned using Se-Al Carbon version 2.0a11 (http://evolve.zoo.ox.ac.uk). PAUP (version 4.40b) (Swofford 2003) was used for parsimony analyses of sequences. Gaps were treated as missing. Trees were created using the stepwise addition with bisection-reconnection as the branch swapping algorithm. Branch confidence was tested using bootstrap analysis (Felsenstein 1985) with 100 replicates for the ITS tree and 500 replicates for the SSU tree. *Decorospora gaudefroyi* (≡ *Pleospora gaudefroyi*) and *Saccharomyces cerevisiae* were used as outgroup taxa for the ITS tree and SSU trees, respectively.

Taxonomy

Monodictys arctica M.J. Day & Currah, **sp. nov.** Figs. 1-10

MYCOBANK #: MB510336

In OAT et PDA, coloniae floccosae, margines leves, interdum discolorationem brunneam medii causantes. In PDA, colonia 35 mm post 35 dies, primum alba ad pallide brunnea, deinde brunnea post 4 dies et argenteo-grisea post 7 dies. Conidia sessilia et lateralia in hyphis vegetativis vel ex extremis ramorum orientia, 5–330 µm longitudine, consistent ex cellulis basalibus blastice productis et ex proliferatione distali cellularum, usque ad 24 numero, quae oriunt ex incremento meristematico; imperfecte globosa quando maturant, oblonga, ellipsoidea vel pyriformia vel inaequaliter vel dichotome ramosa, interdum latiora quam longiora, maxime nigrata (melanisata), levia, crassiter tunicata, constricta prope septa, 12–80 × 12–90 µm. Isolata ex radice Saxifragae oppositifoliae ex insula Ellesmere.

Etymology recognises the collecting locality for the host plant.

Colonies on OAT and PDA floccose with even margins, occasionally causing brown discoloration of medium (Fig. 1). Colony 35 mm after 35 days on PDA, white to light tan at first, becoming brown after four days, and silvery grey

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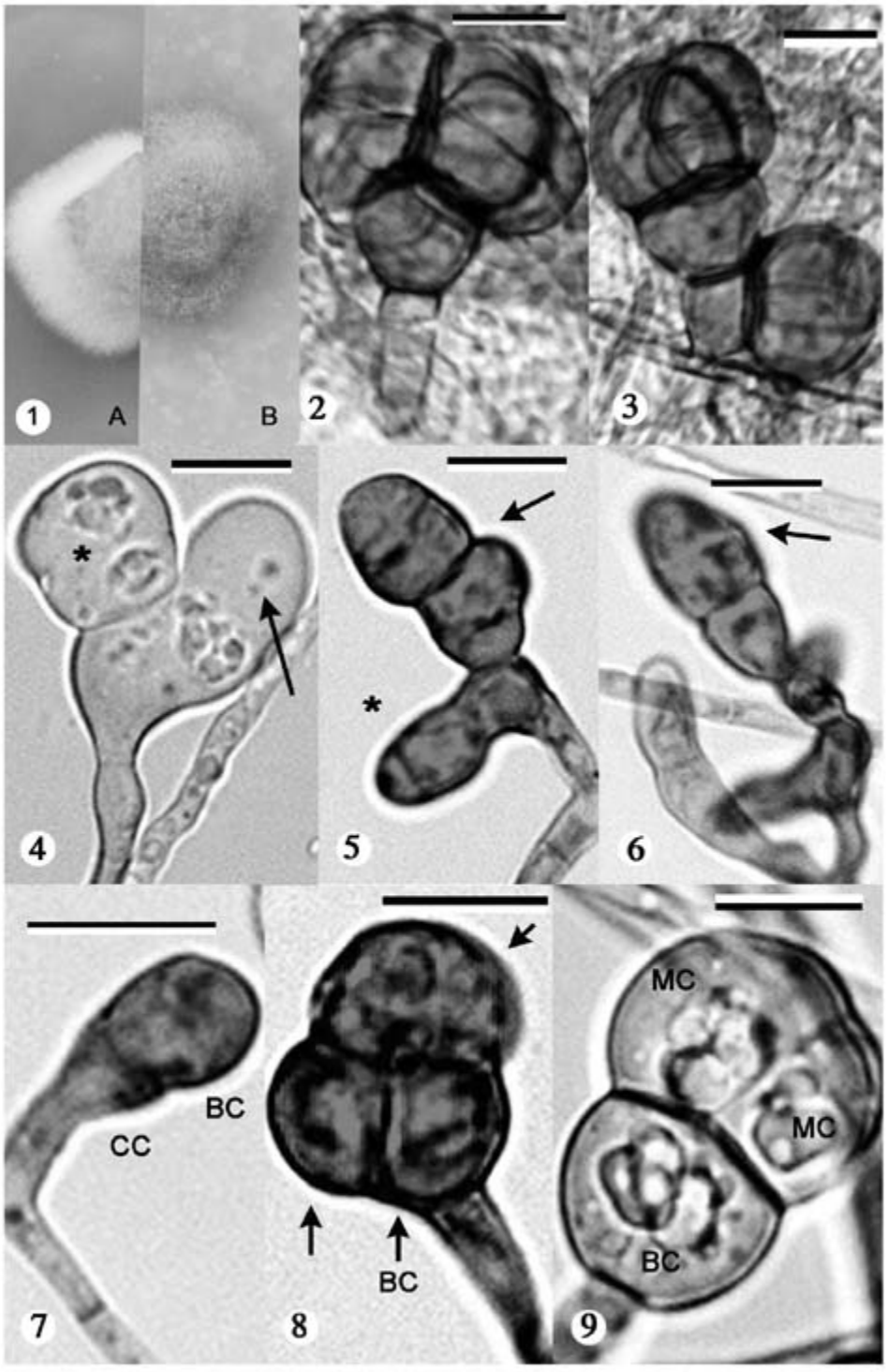
Figs. 1-9 Cultural and morphological features of *M. arctica*. Figure 1. Colony morphology at 12 days of *Monodictys arctica* isolates on (PDA) and (OA). Brown discoloration of medium shown on OA, a) UAMH 10719 on PDA. b) UAMH 10720 (ex-type strain) on OA. **Figure 2.** Globose conidium from a 14 d culture of UAMH 10719 stained in APVA showing the prominent basal cell (*) attached to the conidiogenous cell. **Figure 3.** Conidium from a 14 d culture of UAMH 10719 stained in APVA showing branches. Conidial breadth is larger than length. **Figure 4.** Conidium from a 9 d slide culture of UAMH 10720 cleared in 10% KOH showing development of a second conidial branch (arrow) before division of the first branch (*). **Figure 5.** Conidium from a 7 d slide culture of M.J.D.727 (from same root as UAMH 10723) stained with APVA showing development of a second conidial branch (*) after division of the first branch (arrow). **Figure 6.** Conidium from a 7 d slide culture of UAMH 10718 stained in APVA showing a newly formed septum (arrow). **Figure 7.** Conidium from a 3 d slide culture of M.J.D.727 (from same root as UAMH 10723) stained in APVA showing a basal cell (BC) protruding from the conidiogenous cell (CC). **Figure 8.** Branched conidium from a 7 d culture of UAMH 10718 stained in APVA showing the meristematic initials (MI) of two branches produced by basal cell (BC). **Figure 9.** Conidium from a 9 d slide culture of UAMH 10722 cleared in 10% KOH after division of meristematic initial (MC = meristematic cell). BC = basal cell. All bars = 10µm.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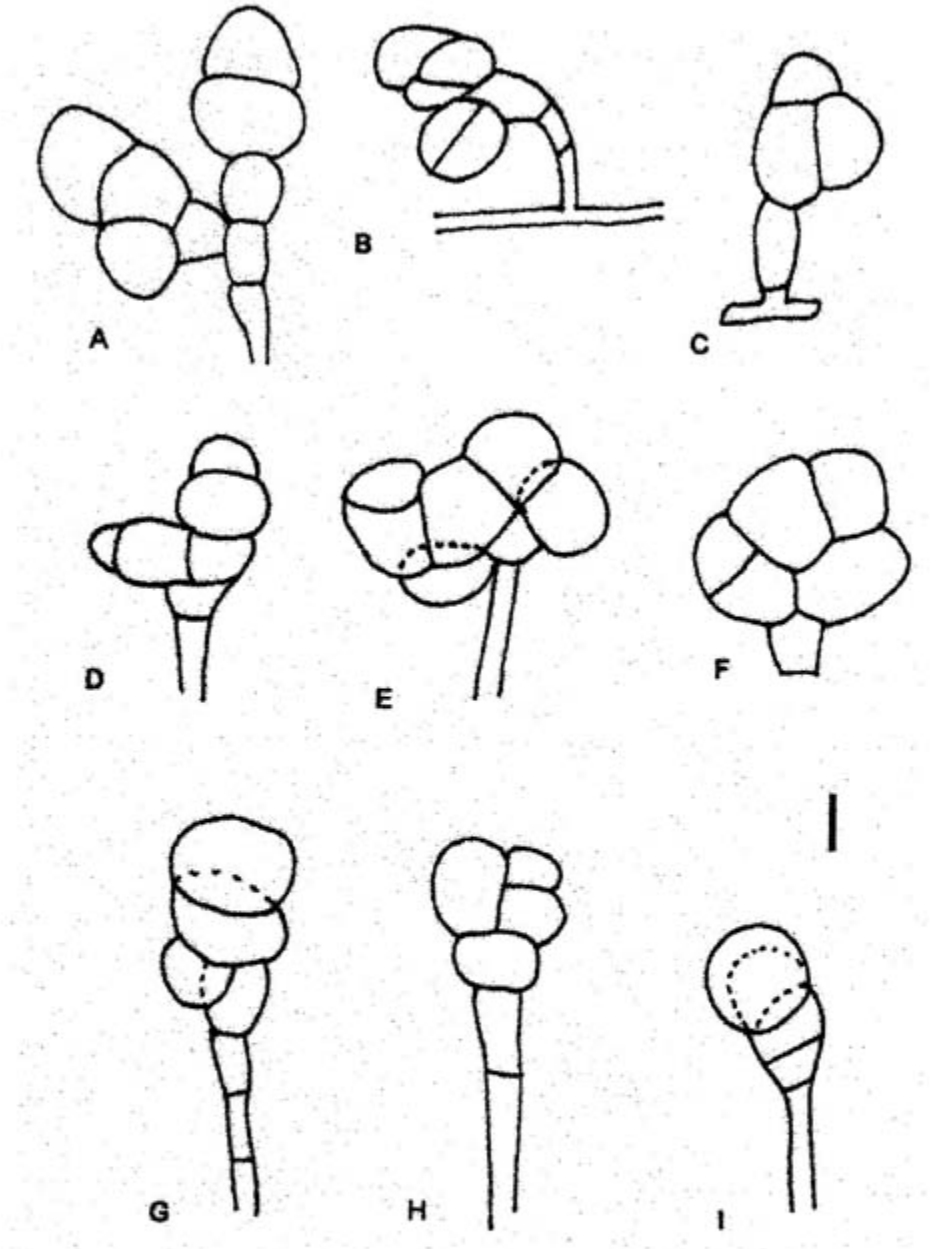

Fig. 10. Line drawings of conidia of *Monodictys arctica*. A. Irregularly shaped branched conidium. B. Branched conidium with second branch just developing. C. Conidium showing two meristematic initials. D. Branched conidium with breadth greater than length. E. Conidium broader than long. F. Roughly globose conidium. G. Roughly ellipsoidal conidium. H. Young, roughly globose conidium. I. Young conidium. Bar = 10 μm

after seven days. Conidia sessile and lateral on vegetative hyphae or arising from lateral branches 5–330 µm in length, consisting of a blastically produced basal cell and a distal proliferation of up to 24 cells arising from meristematic growth (Fig. 2); at maturity, roughly globose, oblong, ellipsoidal, or pyriform to irregularly shaped or dichotomously branched (Figs. 3, 4, 5), deeply pigmented and appearing olive to dark brown, smooth, thick walled, with constrictions at septa, 20–80 × 12–50 µm when length greater than breadth and 12–67 × 20–90 µm when breadth greater than length.

HOLOTYPE – CANADA. Ellesmere Island: Alexandra Fiord, Nunavut (78° 53'N, 75° 55'W), ex roots of *Saxifraga oppositifolia*, 17 Jan 2001, UAMH, a dried culture derived from UAMH 10720 - M.J.D. 121 = K.E.F. 1-S1-OTC3-Saop 3.2)

PARATYPES – dried cultures derived from the following cultures and deposited in the UAMH. All from roots of *Saxifraga oppositifolia* collected at the type locality: 18 Sep 2000, UAMH 10718 - = M.J.D. 73 = K.E.F. 1-S4-OTC3-Saop 4.3; 20 Dec 2000, UAMH 10719 - = M.J.D. 86 = K.E.F. 1-S1-C3-Saop 1.2; 16 Nov 2000, UAMH 10721 - = M.J.D. 192 = K.E.F. 1-S4-OTC2-Saop 4.6; 13 Sep 2000, UAMH 10725 - = M.J.D. 217 = K.E.F. 1-S4-OTC3-Saop 2.2; 25 Sep 2000, UAMH 10722 - = M.J.D. 607 = K.E.F. 1-S4-OTC2-Saop 2.2; 13 Oct 2000, UAMH 10723 - = M.J.D. 729 = K.E.F. 1-S4-OTC2-Saop 1.1B; 13 Oct 2000, UAMH 10724 - = M.J.D. 732 = K.E.F. 1-S4-C1-Saop 4.2.

Results

For both the SSU and ITS regions, isolates shared greatest sequence similarity with *Leptosphaeria* species according to BLAST searches of GenBank. Subsequent parsimony analysis of the SSU DNA placed *M. arctica* in the *Dothideomycetidae* (Fig. 11). The SSU tree included 31 taxa and 1022 characters, of which 740 were constant, 98 parsimony uninformative, and 184 parsimony informative. Nineteen most-parsimonious trees were produced for the SSU region. The consistency index (CI) was 0.612, the retention index (RI) 0.753, and the homoplasy index (HI) 0.388. Analysis of the ITS regions of *M. arctica* and *Leptosphaeria* species placed our isolates in the same clade as *L. dryadophila* (Fig. 12). The ITS tree included 18 taxa and 600 total characters, 336 of which were constant, 85 parsimony uninformative, and 179 parsimony informative. One most-parsimonious tree was produced for the ITS region. The CI was 0.579, the RI 0.490, and the HI 0.421.

Discussion

Our isolates are accommodated within *Monodictys* reasonably well on the basis of morphology even though previous authors have noted that the boundaries among similar genera having pigmented, muriform conidia can be difficult to recognise (Rao and de Hoog 1986, Rodríguez et al. 2001). The genus was erected by Hughes (1958) with *M. putredinis* (Wallr.) S. Hughes as the type species, and is characterised by the production of single, dry, darkly pigmented, multicelled

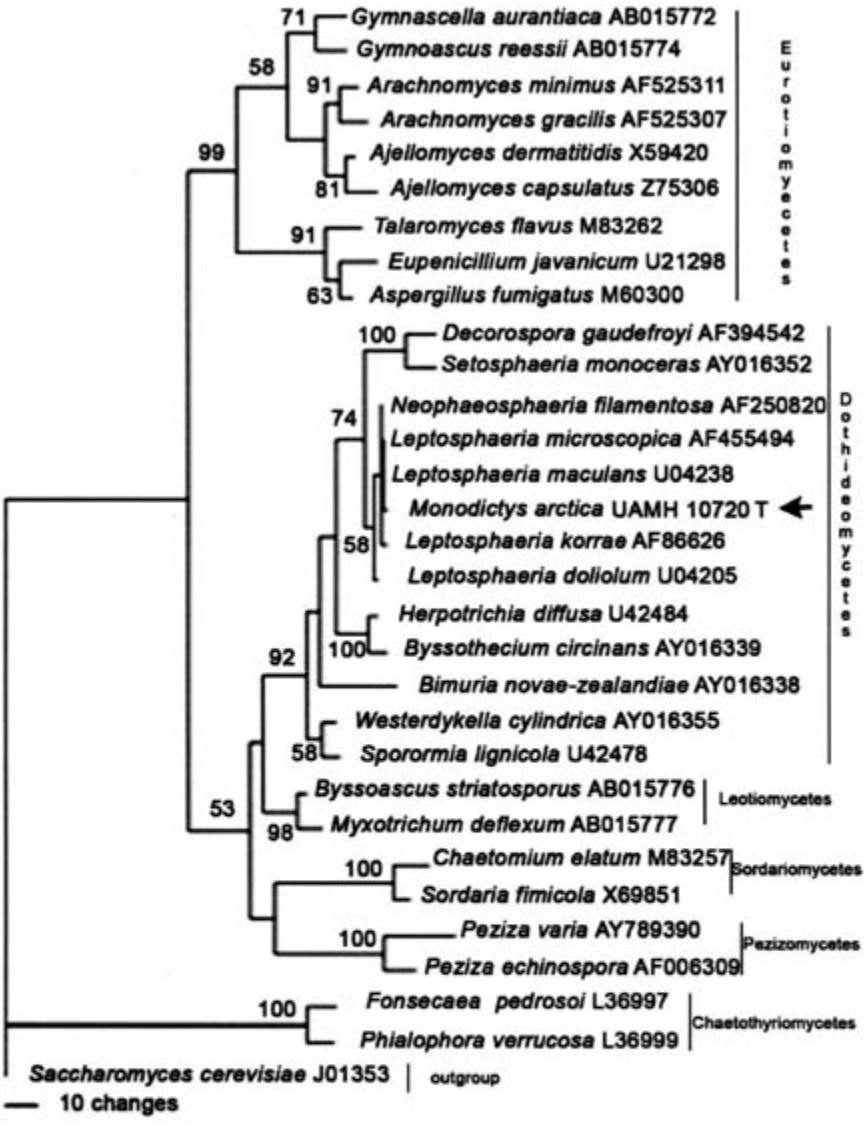

Fig. 11. One of 19 most parsimonious trees based on an analysis of the small subunit rDNA of *Monodictys arctica* and other ascomycetes. The CI = 0.612, RI = 0.752, and HI = 0.38. The outgroup was *Saccharomyces cerevisiae*. Bootstrap support in percentages (for 500 replicates) is shown on branches where support is greater than 50%. T signifies the ex-type strain.

conidia that arise from monoblastic conidiogenous cells. The absence of sporodochia and conidial chains distinguishes members of this genus from developmentally similar taxa (e.g., *Epicoccum, Alternaria* respectively) but the resulting group is heterogeneous and the genus needs re-examination and

revision (Rao and de Hoog 1986, Rodríguez et al. 2001). *Monodictys arctica* is distinguished from others in the genus by having smooth, mostly irregularly shaped conidia that are occasionally branched. The conidia of *M. antiqua* (Corda) S. Hughes and *M. lepraria* (Berk.) M.B. Ellis are somewhat similar in being lobed (Ellis 1976) but are larger, up to 75 × 25 µm in *M. lepraria* and 100 × 50 µm in *M. antiqua*.

During conidium development in *M. arctica*, the conidiogenous cell swells and produces a transverse septum (Fig. 6) that delineates a basal cell (Wang 1990) (Fig. 7), which in turn produces one or two cells that serve as meristematic initials (Fig. 8). Meristematic initials are subsequently partitioned by septa that form on irregular, i.e., non-orthogonal, planes of division, but resultant cells ("meristematic cells," Fig. 9) enlarge so that the component cells of the mature conidium are similar in size. The basal cell persists in the mature conidium and is recognised by being less heavily pigmented than the more distal meristematic portion. This developmental sequence agrees with previous observations made by Hughes (1953) and Ellis (1971) on *M. paradoxa*. By observing longitudinal sections through the conidium, and the subtending conidiophore in *M. paradoxa* (Corda) S. Hughes, using transmission electron microscopy, Wang (1990) determined that conidiogenesis involved percurrent proliferation of the conidiogenous cell, which resulted in the formation of an inconspicuous annellophore. This process was not detected in *M. arctica* using light microscopy. We also did not see evidence of rhexolytic dehiscence or remnants of the conidiogenous cell forming a hilum (Samuels 1980). Further observations using ultrastructural techniques would be useful in clarifying the mode of conidiogenesis in our new species and similar observations across a range of species of *Monodictys* could be of value in clarifying the conceptual limits of the genus.

Analysis of SSU sequences places *M. arctica* within the *Dothideomycetidae*. Only two other species of *Monodictys*, *M. pelagica* (T. Johnson) E.B.G. Jones and *M. castanea* (Wallr.) S. Hughes, are represented by sequences in GenBank and these show affinities with the *Sordariomycetidae*. However, links between the Loculoascomycetes (sensu Barr and Huhndorf 2001) and *Monodictys* have been reported. For example, Samuels (1980) observed conidia resembling *M. putredinis* developing in cultures derived from ascospores of *Ohleria brasiliensis* (*Melanommataceae*). Unfortunately, there are no sequences for either *M. putredinis* or *O. brasiliensis* in GenBank.

Phylogenetic analysis of the ITS region suggests that *M. arctica* is quite likely the anamorph of a species of *Leptosphaeria*, a loculoascomycete genus known from a broad range of plants and habitats, but otherwise having pycnidial anamorphs (e.g., in *Coniothyrium*, *Diplodina*, *Haplosporella*, *Phaeoseptoria*, *Phoma*, *Scolecosporiella*, *Septoria*, and *Stagonospora*; Dennis 1981, Farr et al. 1989). Pycnidia were not observed in our cultures but conidial development

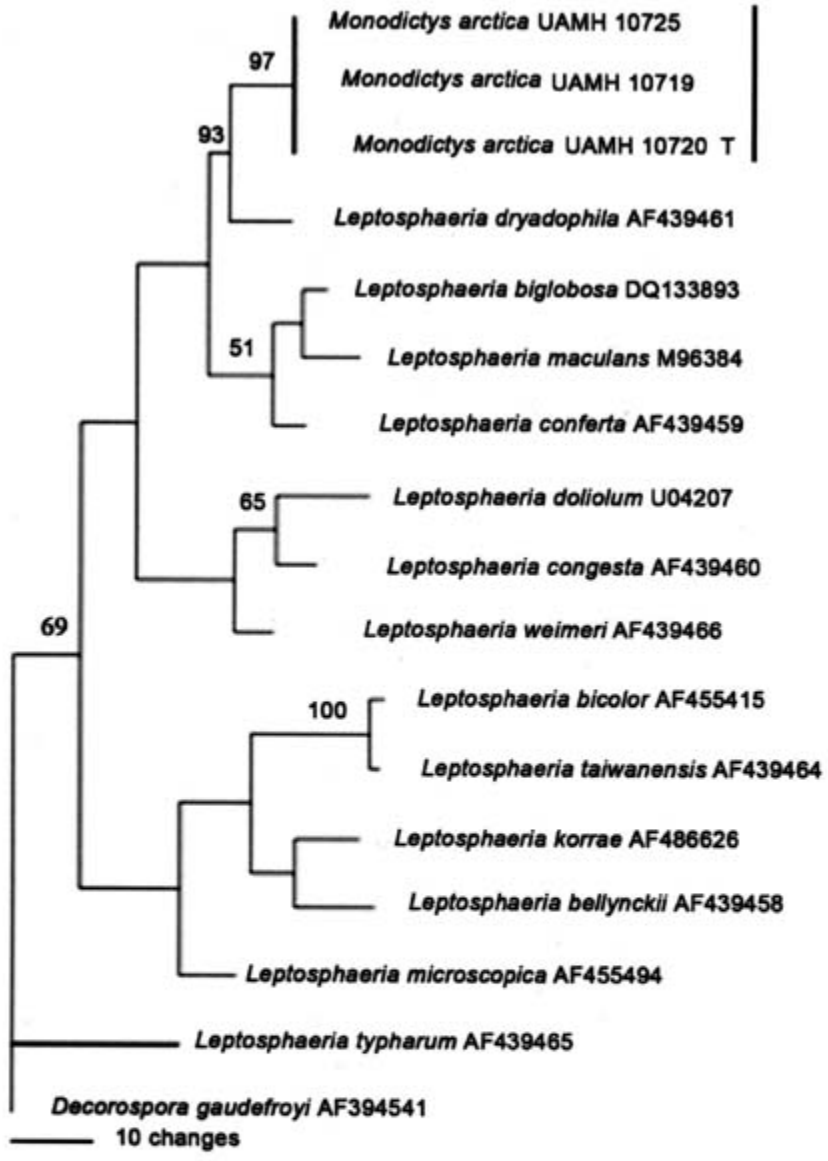

Fig. 12. The most parsimonious tree based on an analysis of the internal transcribed spacer region of *Monodictys arctica* and members of *Leptosphaeria*. The CI = 0.579, RI = 0.490, and HI = 0.721. The outgroup was *Decorospora gaudefroyi*. Bootstrap support (100 replicates) is shown on branches where support is greater than 50%. T signifies the ex-type strain.

in *Monodictys* resembles stages in the development of pycnidia by *Phoma* and *Asteromella*. Also, the *Monodictys*-like anamorph of *Tubeufia amazonensis* (*Tubeufiaceae*) often forms pycnidial locules bearing phialides and single-celled conidia (Samuels 1980). Finally, the formation of pseudoparenchymatous balls,

reminiscent of large dictyoconidia, have been associated with the appearance of pycnidia and ascomata in *Leptosphaeria* (Samuels 1980).

The closest genetic match to *M. arctica* (94% similar to the ex-type strain, UAMH 10720) is *L. dryadophila* Huhndorf (≡ *Melanomma dryadis* Johanson). The close genetic similarity between these two species and the similar habitat, i.e., on subfrutescent perennial species native to arctic or alpine habitats, suggest these taxa might be sibling species but additional data supporting this supposition are missing. For example, it is unknown if *L. dryadophila*, which produces its ascostromata on the leaves and flowers of *Dryas octopetala* and *D. integrifolia* (Huhndorf 1992, Chlebicki 2002), is systemic and in the roots of these hosts. Furthermore, and as far as we are aware, an anamorph is unknown for *L. dryadophila*. Three other species of *Leptosphaeria*, i.e., *L. brachyasca* Rostr., *L. hyperborea* (Fuckel) Berl. & Voglino, and *L. oreophila* Sacc. (Connors 1967, Farr et al. 1989) have been reported from species of *Saxifraga* but neither cultural nor sequence data are available for these taxa.

Whether *M. arctica* inhabits root cortices in the same relatively harmless manner as other dark septate endophytes such as *Phialocephala fortinii*, *Leptodontidium orchidicola*, and *Scytalidium vaccinii*, all of which were among the isolates examined from the four angiosperm hosts, is unknown. Pattern of occurrence, i.e., in one of four plant species collected from within and outside the OTCs, suggests that host identity had a stronger influence than the experimental treatments. Direct examination of roots of *Saxifraga oppositifolia* infected with *M. arctica* is required to determine the colonisation pattern and whether the fungus is a pathogen or relatively harmless parasite. Furthermore, close inspection of host shoot tissues might indicate the presence of a previously overlooked loculoascomycete teleomorph similar to *Leptosphaeria dryadophila*.

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