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Title: *Mucor nidicola* sp. nov., a novel fungal species isolated from an invasive paper wasp nest.

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*The GenBank accession numbers for the ITS1-5.8rDNA-ITS2 sequences of the *Mucor* spp. strains examined in this study are provided in a supplementary table (Table S1).

†The ex-type living culture of *Mucor nidicola* sp. nov. has been deposited in the USDA Agricultural Research Service Culture Collection under the designation NRRL 54520, and in the Centraalbureau voor Schimmelcultures under the designation CBS XXXXXX. The holotype and ex-type culture has been deposited in the University of Alberta Microfungus Collection and Herbarium under the designation UAMH 11442. The MycoBank accession number for *M. nidicola* is MB 5619980

Summary

Mucor nidicola sp. nov. is a novel mucoralean fungus isolated from a nest of the invasive paper wasp, *Polistes dominulus*. Phylogenetic analysis based on the internal transcribed spacers (ITS) and 5.8S rRNA gene sequences, along with physiological tests, revealed that this is a species within the genus *Mucor*. The new species also includes a representative that had

previously been characterized as part of the *M. hiemalis* complex. Unlike the type strain of *M. hiemalis*, these two strains can grow at 37 °C and sporulate at 35 °C. Here we present a partial resolution of the *M. hiemalis* species complex and identify the novel species with the proposed name *Mucor nidicola*.

Research Article

Paper wasps are nearly globally distributed insects that create nests of macerated cellulose pulp, foraged by wasps from leaves, grass, cardboard, and decomposing plant matter (Evans & West-Eberhard, 1970). Because of the ubiquity of fungal saprophytes in decomposing plant matter (reviewed in Ribes *et al.,* 2000), it is not surprising that multiple *Mucor* species have been isolated in the few mycobiota assessments conducted on paper wasp nest material (Jayaprakash & Ebenezer, 2010; Fouillaud & Morel, 1995). While ubiquitous in distribution, species of *Mucor* are valued particularly for their fast growth and novel metabolic pathways. Various *Mucor* species are used in applications such as bioremediation (Purnomo *et al.,* 2010; Srinivasan & Viraraghavan, 2010; Jabasingh & Pavithra, 2010), and the production of biofuels (Alam *et al.,* 2009), bioprotein (Jamal *et al.,* 2007), and pharmaceutical and industrial enzymes and chemicals (reviewed in Yazdi *et al.,* 2006). Some *Mucor* species are even used as a model for drug metabolism (Moussa *et al.,* 1997).

An assortment of fungal species was isolated from the nests of the invasive paper wasp, *Polistes dominulus*, in Massachusetts, USA, as part of a biodiversity study. Initial sequence analysis of the ITS region, the standard phylogenetic marker used for Mucorales identification (Balajee *et al*., 2009), and subsequent phylogenetic and phenotypic studies of these strains, revealed the presence of a previously uncharacterized species related to *M. hiemalis* and *M. irregularis*. Here we propose this novel species of *Mucor*: *Mucor nidicola* sp. nov.

Isolation and Characterization

Active nests of the invasive paper wasp *P. dominulus* were aseptically collected in Medford, Massachusetts, USA in August, 2008. Nest material was homogenized in a dilute phosphate buffered saline solution and maintained at 15 °C for six months prior to fungal isolation. Samples were plated on potato dextrose agar (PDA) (Difco). After incubating at approximately 24 °C for 72 h under diffuse light, morphologically distinct colonies were further purified on PDA.

DNA was extracted and purified directly from fungal colonies following the Fast DNA Kit protocol (Bio101), with a minor modification: we repeated the homogenization step three times with a FastPrep FP120 instrument (Thermo Savant). DNA was quantified by GeneQuant Pro (Amersham Pharmacia Biotech). The internal transcribed spacer (ITS) region of the nuclear rRNA gene was amplified with the primer pair ITS5 and ITS4 (White *et al.,* 1990). The PCR mix (25 µl) included 10 mM Tris-HCl (pH 8.3), 50 mM KCl and 2.5 mM $MgCl_2$ (10X Perkin-Elmer buffer II plus $MgCl_2$ solution Roche Molecular Systems), 100 µM each dNTP (Promega), 1 µM of each primer and 1.5 U of Ampli *Taq* DNA polymerase (Roche). The amplification program included an initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing for 1 min at 55 °C, and extension for 1 min at 72 °C. Subsequent products were purified with an Illustra GFX ™ PCR DNA and Gel Band Purification Kit (General Electric Healthcare) and stored at -20 °C until they were used in sequencing. PCR products were sequenced by using the same primers used for amplification and following the *Taq* DyeDeoxy Terminator Cycle Sequencing Kit protocol (Applied Biosystems). Reactions were run on a 310 DNA sequencer (Applied Biosystems). Consensus sequences were obtained using the

Autoassembler program (PerkinElmer-Applied Biosystems) and Seqman software (Lasergene package, DNASTAR).

Clustal X v.1.8 was used to align the sequences, followed by manual adjustments with a text editor (Microsoft Office Word 2003, version SP3). Once the sequences were aligned and adjusted, the similiarity percentages were manually calculated as the difference in the number of nucleotides between sequences A and B divided by the number of total bases of these sequences x 100. For additional analysis of the genes, we used the software program MEGA 4.0. The maximum composite likelihood algorithm was used to determine the evolutionary distances between sequences. Phylogenetic trees were generated using the neighbor-joining (NJ) method. Gaps were treated by the pairwise deletion option of MEGA. Support for internal branches was assessed by a search of 1000 bootstrap (BS) replications.

Isolates were subcultured on PDA (Pronadisa) and malt extract agar (MEA; 10 g of malt extract, 20 g of agar, and 1000 ml of distilled water), and incubated at room temperature (25 °C) for 2–5 days. Microscopic features were determined in mounts in lactic acid. Photomicrographs were taken using a Zeiss Axio Imager M1 light microscope. All isolates were characterized morphologically following traditional criteria (Schipper, 1973). Color notations in parentheses are from Kornerup & Wanscher (1978). Growth rates of the isolates at different temperatures (4, 7, 15, 25, 30, 35, 37, 40, 42, 45 and 50 °C) were determined on 90 mm diameter PDA Petri dishes that had been inoculated at the center. Colony diameters (in mm) were measured daily, for up to 10 days.

Results

Using methods outlined above, the length of the amplicon of the ITS region of the strain designated F53 was determined to be 583 bp. The type species of the genus *Mucor*— *M.*

mucedo— was used as a natural outgroup to root the phylogenetic tree (Figure 1). In the resulting phylogram, isolate F53 formed a clade with the unnamed species currently known as *M. hiemalis* f. *corticola*, with several strains of related *M. hiemalis* f. *hiemalis*, and with the type strains of *M. hiemalis* (var. *hiemalis*), *M. irregularis* (previously *Rhizomucor variabilis* var. *variabilis*), and *M. luteus*. However, isolate F53 was genetically distinct from all of these strains, as its ITS region nucleotide sequence differed by more than 2 % (Alvarez *et al*., 2009), with the exception of strain *M. hiemalis* f. *hiemalis* CBS 638.67, with which it formed a terminal branch supported by a 100 % BS value (Figure 1). Strain CBS 638.67, isolated from a greenhouse soil sample from the Netherlands, had been previously reported by Schipper (1973) as '*M. spec. 2.*' Isolates F53 and CBS 638.67 exhibited similar morphological and physiological features and were able to grow at 37 ºC and sporulate at 35 ºC. The subclade in which strains F53 and CBS 638.67 were placed (BS 73 %), includes two other branches. The first branch, in a basal position, includes only the type strain of *M. irregularis* CBS 103.93, whereas the second is a sister branch of F53 and CBS 638.67 (BS lower than 70%). This sister branch (BS 100 %) includes strains CBS 975.68A, CBS 975.68B, and CBS 976.68— all deposited in the CBS as *M. hiemalis* f. *hiemalis*. These three isolates were also designated '*M. spec. 2'* by Schipper (1973), but their ITS rRNA sequences, and those of strains F53 and CBS 638.67 differed by 29 bp (6 %). Table S2 shows the similarity percentage between the ITS region nucleotide sequences of these strains. On the basis of our results, it is clear that *M. hiemalis sensu lato* represents a species complex.

The type strain of *M. hiemalis* (CBS 201.65^{NT}) clustered with strain CBS 106.09, which was deposited as *M. hiemalis* f. *corticola* (Figure 1). Strain CBS 412.71, representing *M. hiemalis* f. *silvaticus*, was placed outside of the *M. hiemalis* complex. Surprisingly, the type

strain of *M. genevensis* (CBS 114.08^T), a species morphologically related to the *M. hiemalis* species group, was only distantly related to the species within this group (Figure 1).

Isolate F53, described here as the type strain of *M. nidicola*, is morphologically similar to other species of the *M. hiemalis* complex. All produce yellowish to orange colonies and tall, mostly unbranched sporangiophores, rarely with a single branch or slightly branched sympodially, ending with a yellowish, brownish or brownish-black sporangium with mostly ellipsoidal-shaped sporangiospores (Figure 2). However, *M. nidicola* grows and sporulates at 30 ºC, while the type strain of *M. hiemalis* does not. Moreover, *M. nidicola* differs from *M. hiemalis* f. *corticola*, *M. luteus*, *M. hiemalis* f. *silvaticus*, and *M. genevensis* in its ability to sporulate at 35 ºC and to grow at 37 ºC. This fact was previously noticed by Schipper (1973), in several strains of *M. hiemalis* f. *hiemalis* that she designated '*M. spec. 2*'. The maximum temperature of growth and sporulation are important taxonomic tools, because they permit the separation of phylogenetically different, but morphologically similar mucoralean fungi, such as certain species belonging to the genera *Mucor* and *Rhizomucor* (Alvarez *et al*., 2009).

Although the differences among the species within the *M. hiemalis* complex are not great, as they are all members of the same complex, *M. nidicola* can be morphologically and physiologically differentiated from the closely related species or varieties of the complex. *M. hiemalis* f. *corticola* produces cylindrical-ellipsoidal sporangiospores, which are narrow ellipsoidal to nearly fusiform in *M. luteus*, and cylindrical in *M. hiemalis* f. *silvaticus*, whereas they are mostly ellipsoidal, kidney-shaped, and irregular in *M. nidicola*. Moreover, *M. hiemalis* f. *silvaticus* produces blackish brown sporangia, which are much paler in all other *formae* of *M. hiemalis*. Morphologically, the closest taxon to *M. nidicola* is *M. hiemalis* f. *hiemalis*, although the sporangiospores of this species are regularly ellipsoidal with a flattened side whereas in *M.*

143 *nidicola* they are ellipsoidal, reniform, and irregularly-shaped. The most significant difference
144 between these species is the ability of *M. nidicola* to grow and sporulate at higher temperatures,
145 i.e. 37 ºC and 35 ºC, respectively— the corresponding temperatures for *M. hiemalis* f. *hiemalis*
146 are 30 ºC and 25 ºC, respectively.

147 *Mucor nidicola* differs morphologically from *M. irregularis*, as the later produces
148 sporangiospores that are highly variable in shape and larger in size (2.5–16.5 x 2.0–7.0 µm).
149 Moreover, *M. irregularis* produces rhizoids and profusely branched sporangiophores, whereas
150 the rhizoids are absent and the sporangiophores are mostly unbranched in *M. nidicola*.

151 *M. nidicola* and all the other species of the *M. hiemalis* complex differ from *M.*
152 *genevensis* in that the latter species is homothallic, producing zygospores from colonies derived
153 from single sporangiospores.

154

155 **Conclusion**

156 Based on phylogenetic and phenotypic assessments, the species *Mucor nidicola* is
157 proposed. This species includes the type strain F53 and the strain currently designated as *M.*
158 *hiemalis* f. *hiemalis* CBS 638.67. Sequence comparisons with those available in GenBank
159 suggest at least one strain isolated by Pan & May (2009) as an endophyte of corn (*Zea mays*)
160 (GenBank accession FJ210517), represents an additional member of this species. The varied
161 locations from which members of this species have been isolated: a paper wasp nest in
162 Massachusetts, USA; as a corn endophyte in Minnesota, USA (Pan & May, 2009); and on a glass
163 walled herbarium in the Netherlands (Schipper 1973), suggest that in keeping with many *Mucor*
164 species, *M. nidicola* has a cosmopolitan distribution.

Species description. *Mucor nidicola* Madden, Stchigel, Guarro, Sutton, et Starks, sp. nov. Figs. 1-2. MycoBank MB 5619980.

Ad 25 °C *in agaro cum decocto malturorum* (MEA) *coloniae Petri-patellas in die quarto, luteola vel aurantio–grisea* (M. 5A4 to 5B4), *adversum aurantium vel auratio-brunneum. Mycelium* 5–10 mm *altum, primo hyalinum cito aurantium ex guttulis oleosis praesens. Sporangiophora erecta, simplicia vel* 1–2 *ramosa; rami sporangiophoris* 500–2000 μm *longi*, 10–15 μm *lati, cum septum unicus ad basim, hyalini vel lutei, cum sporangio terminatibus nonapophysati. Sporangia globosa, cum parietibus subpersistentibus, lente tabidis vel disruptis, levitunicatis vel verrucosi, ad* 30–70 μm *in diam, luteola vel aurantio-brunnea. Columellae globosae vel subglobosae, collaria distincta,* 15–40 x 20–45 μm, *hyalina vel pallide brunnea. Sporangiosporae praecipue ellipsoideae, sed reniformis vel irregulares*, 3–10 x 2–6 μm, *pallide griseo-brunnea, levae et tenui- vel crassitunicatae. Zygosporae ignotae. Typus:* F53^{T} (=NRRL 54520^{T} =UAMH 11442^{T} =CBS XXXXXX^{T}) *Holotypus conservatur in collectiones curturorum* USDA Agricultural Research Service (NRRL), University of Alberta Microfungus Collection and Herbarium (UAMH), *et* Centraalbureau voor Schimmelcultures (CBS).

Colonies cottony, filling Petri dish after four days incubation at 25 ºC on MEA, light orange to grayish-orange (M. 5A4 to 5B4), reverse orange to brownish-orange (M. 5A6 to 5C5). Colonies about 5–10 mm high, at first white, becoming yellowish-orange due to the presence of numerous cytoplasmic oil droplets. Hyphae branched, non-septate when young, becoming septate with age, 5–20 μm diam. Sporangiophores erect, simple or 1–2 branched, arising directly from superficial and aerial hyphae; branches 500–2000 μm long, 10–15 μm wide, one septate at base, colorless to yellowish, simple, terminating in a non-apophysate sporangium. Sporangia multisporate, globose, wall slowly dissolving or broken, 30–70 μm diameter, yellowish to

188 brownish, smooth-walled to warty. Columellae globose to subglobose, non-collapsing, 15–40 x
189 20–45 µm, hyaline to pale brown, collar evident. Sporangiospores mostly ellipsoidal, but also
190 kidney-shaped or irregular, 3–10 x 2–6 µm ($\overline{X}$ = 5.5 x 3.0 µm), pale greyish-brown, smooth- and
191 thin- to thick-walled. Chlamydospores abundant, terminal and intercalary, single or in chains up
192 to 14 chlamydospores, hyaline, globose, barrel-shaped to cylindrical or irregular, 10–30 µm long,
193 5–15 µm wide, thick-walled, formed on vegetative hyphae. Zygospores unknown.
194 The optimal growth temperature is 25 ºC, but it grows and sporulates well between 15
195 and 35 ºC. At 35 ºC it also grows and sporulates (45–50 mm after four days), but produces
196 sporangiophores with shorter branches and broadly ellipsoidal to subglobose sporangiospores. It
197 displays poor growth at 37 ºC and no growth at 7 ºC or 40 ºC.

198 HOLOTYPUS: UAMH 11442, a dried culture isolated in February, 2009, from a *P.*
199 *dominulus* nest in Medford, MA, USA. Ex-holotype culture, F53 (= NRRL 54520= UAMH
200 11442= CBS XXXXXX).

201 **Etymology:** *nidicola:* ni.di'co.la. L. *nidus*, nest; L. suff. –cola (from L. n. *incola*),
202 inhabitant, dweller; N.L. n. *nidicola*, nest-dweller, referring to the location from which the type
203 strain of this species was isolated: a nest of the paper wasp, *Polistes dominulus*.
204
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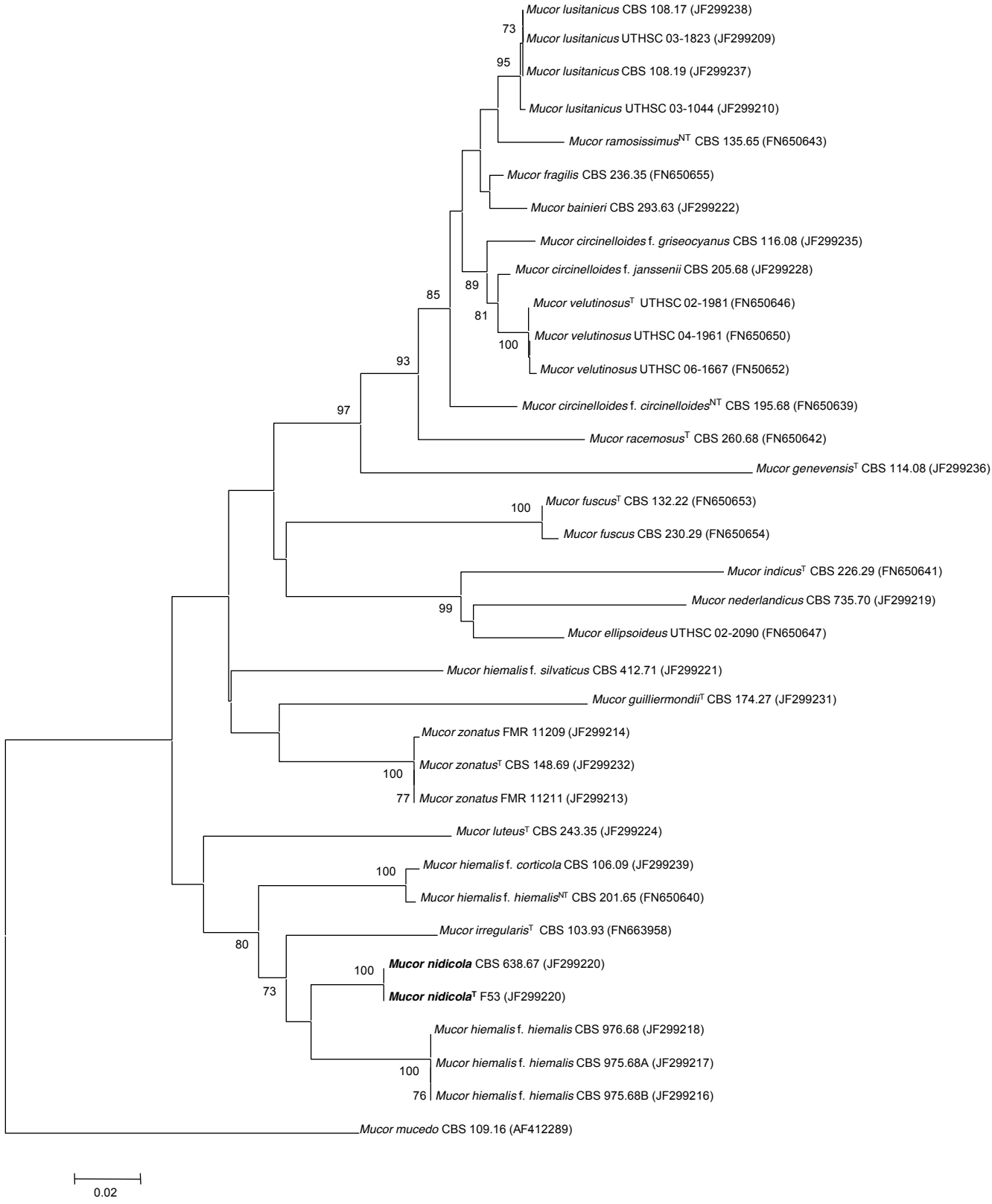
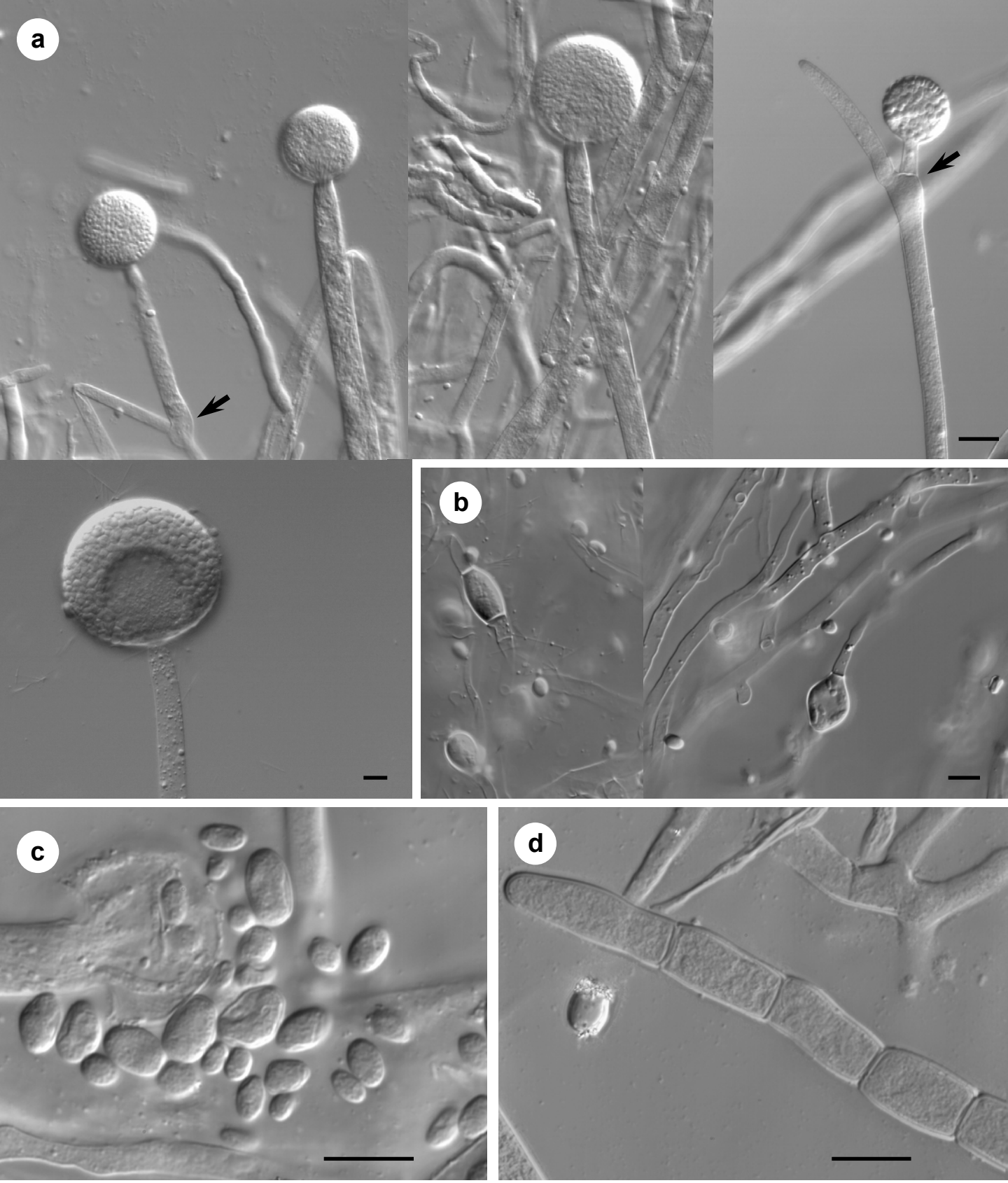
Figure 1. Neighbor-joining tree based on maximum composite likelihood corrected nucleotide distances among the ribosomal internal transcribed spacer (ITS) regions and 5.8S rRNA gene sequences of the strains of *Mucor* spp. studied. Bootstrap support values above 70% are indicated at the nodes. The bar indicates genetic distance.

Figure 2. *Mucor nidicola*, F53^{T}. (a) Sporangiophores (arrows indicate where the branches arise from the conidiophore) with sporangia (b and d) Chlamydospores. (c) Sporangiospores. Bars: 20 μm.

Table S1. Strain sequences referenced within this study, and their respective GenBank accession numbers.

289 **Table S2.** ITS region nucleotide sequence similarities among *M. nidicola* and related species.


Mucor lusitanicus CBS 108.17 (JF299238)
73
Mucor lusitanicus UTHSC 03-1823 (JF299209)
95
Mucor lusitanicus CBS 108.19 (JF299237)
Mucor lusitanicus UTHSC 03-1044 (JF299210)
*Mucor ramosissimus*NT CBS 135.65 (FN650643)
Mucor fragilis CBS 236.35 (FN650655)
Mucor bainieri CBS 293.63 (JF299222)
Mucor circinelloides f. *griseocyanus* CBS 116.08 (JF299235)
Mucor circinelloides f. *janssenii* CBS 205.68 (JF299228)
89
85
*Mucor velutinosus*T UTHSC 02-1981 (FN650646)
81
Mucor velutinosus UTHSC 04-1961 (FN650650)
100
93
Mucor velutinosus UTHSC 06-1667 (FN50652)
97
Mucor circinelloides f. *circinelloides*NT CBS 195.68 (FN650639)
*Mucor racemosus*T CBS 260.68 (FN650642)
*Mucor genevensis*T CBS 114.08 (JF299236)
100
*Mucor fuscus*T CBS 132.22 (FN650653)
Mucor fuscus CBS 230.29 (FN650654)
*Mucor indicus*T CBS 226.29 (FN650641)
Mucor nederlandicus CBS 735.70 (JF299219)
99
Mucor ellipsoideus UTHSC 02-2090 (FN650647)
Mucor hiemalis f. *silvaticus* CBS 412.71 (JF299221)
*Mucor guilliermondii*T CBS 174.27 (JF299231)
Mucor zonatus FMR 11209 (JF299214)
100
*Mucor zonatus*T CBS 148.69 (JF299232)
77
Mucor zonatus FMR 11211 (JF299213)
*Mucor luteus*T CBS 243.35 (JF299224)
100
Mucor hiemalis f. *corticola* CBS 106.09 (JF299239)
Mucor hiemalis f. *hiemalis*NT CBS 201.65 (FN650640)
*Mucor irregularis*T CBS 103.93 (FN663958)
80
100
Mucor nidicola CBS 638.67 (JF299220)
73
***Mucor nidicola*T** F53 (JF299220)
Mucor hiemalis f. *hiemalis* CBS 976.68 (JF299218)
100
Mucor hiemalis f. *hiemalis* CBS 975.68A (JF299217)
76
Mucor hiemalis f. *hiemalis* CBS 975.68B (JF299216)
Mucor mucedo CBS 109.16 (AF412289)
0.02


a
b
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