Nematode-Trapping Fungi

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This manuscript provides an account of nematode-trapping fungi including their taxonomy, phylogeny and evolution. There are four broad groups of nematophagous fungi categorized based on their mechanisms of attacking nematodes. These include 1) nematode-trapping fungi using adhesive or mechanical hyphal traps, 2) endoparasitic fungi using their spores, 3) egg parasitic fungi invading nematode eggs or females with their hyphal tips, and 4) toxin-producing fungi immobilizing nematodes before invasion The account briefly mentions fossil nematode-trapping fungi and looks at biodiversity, ecology and geographical distribution including factors affecting their distribution such as salinity. Nematode-trapping fungi occur in terrestrial, freshwater and marine habitats, but rarely occur in extreme environments. Fungal-nematodes interactions are discussed the potential role of nematode-trapping fungi in biological control is briefly reviewed. Although the potential for use of nematode-trapping fungi is high there have been few successes resulting in commercial products.

Key words – Ascomycetes – Biocontrol – Biodiversity – Fossil fungi – Fungi – Nematodes – Phylogeny

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Table of contents

Introduction

There are four broad groups of nematophagous fungi categorized based on their mechanisms of attacking nematodes (Liu et al. 2009). These include (1) nematode-trapping fungi using adhesive or mechanical hyphal traps, (2) endoparasitic fungi using their spores, (3) egg parasitic fungi invading nematode eggs or females with their hyphal tips, and (4) toxin-producing fungi immobilizing nematodes before invasion (Kendrick et al. 2001, Liu et al. 2009).

The first nematode-trapping fungus to be described was *Arthrobotrys oligospora* Fresen. in 1852, but at that time its predatory habit was unknown. The predatory habit was first observed 36 years later by Zopf (1888). Since nematode-trapping fungi have considerable potential for biological control of nematodes, there have been extensive studies and reviews on their taxonomy, phylogeny, biology, and ecology (Cooke 1963, Kerry 1987, Sayre & Walter 1991, Sikora 1992, Kerry & Hominick 2002, Morton et al. 2004, Dong & Zhang 2006, Sikora et al. 2007). In this review, aspects such as taxonomy, phylogeny, diversity, and ecology of nematode-trapping fungi and their potential in use in biocontrol of nematodes are reviewed.

Taxonomy, phylogeny and evolution of nematode-trapping fungi

Background of the generic classification

Nematode-trapping fungi are a heterogeneous group of anamorphic ascomycetes where species are defined primarily based on conidial characteristics such as size, septation, and type of conidiogenous cells (Oudemans, 1885, Subramanian, 1963). This has resulted in considerable ambiguity and confusion in intergeneric classification of these organisms. Since the discovery of predacious activity in *Arthrobotrys oligospora* (Zopf, 1888), nematode-trapping fungi have attracted much interest amongst mycologists. Many generic names have been given to nematode-trapping fungi but the basis on which species were circumscribed to different genera was unclear and subjective. Since 1930, nematode-trapping fungal have been described and classified mostly in *Arthrobotrys* Corda, *Dactylaria* Sacc, and *Dactylella* Grove.

Corda (1839) established the genus *Arthrobotrys* with *A. superba* Corda as the type species. Characteristics of this genus are hyaline conidiophores which produce conidia asynchronously on short denticles at swollen conidiogenous heads or clusters of pronounced denticles (De Hoog 1985). Conidia are subhyaline, obovoidal or clavate and (0–)1(–6)-septate. Trapping devices are constricting rings, adhesive nets, hyphae or adhesive knobs (De Hoog 1985). Due to these broad morphological criteria the delimitation from *Arthrobotrys* is sometimes problematic, particularly in *Dactylella* species which form more than one or two conidia on each conidiophore (Cooke & Dickinson 1965). Based on this reason, Van Oorschot (1985) restricted *Dactylella* to species with fusiform, multi-septate conidia, while *Arthrobotrys* species generally have ovoidal to clavate, 0–3-septate conidia. Van Oorschot (1985) recognized 28 species of *Arthrobotrys*. Schenck et al. (1977) expanded the genus to 47 species. After Schenck et al. (1977) transferring all predacious species formerly described in *Dactylaria* to *Arthrobotrys*, *Dactylaria* was no longer tenable for nematode-trapping species. Recent classification based mostly on DNA sequence data has resulted in the transfer of species characterized by adhesive networks to *Arthrobotrys* (Scholler et al. 1999). Currently, there are 120 records of *Arthrobotrys* species but this includes basionyms and synonyms (Index Fungorum, 2011). A more realistic estimate is 63 (Kirk et al. 2008).

Monacrosporium was introduced by Oudemans (1885) with two species, *Monacro-*

sporium elegans Oudem. and *M. subtile* Oudem. This generic name has been used by many authors for several species following the opinion of Oudemans (1885). Subramanian (1964) later selected *M. elegans* as lectotype species for this genus, highlighting the inflated middle cell of the conidia as the distinguishing generic criterion, and transferred a large number of nematode-trapping fungi from *Dactylella* species to *Monacrosporium*. Rubner (1996) revised most predacious hyphomycetes in *Dactylella* and *Monacrosporium* to delimitate between the two genera. Scholler et al. (1999), however, proposed a new genus concept for predatory anamorphic Orbiliaceae and the genus *Monacrosporium* was discarded. Many nematode-trapping fungal species are homeless and *Monacrosporium* is used as their current name. Currently, 74 taxa are listed in Index Fungorum (Index Fungorum, 2011), while Kirk et al. (2008) estimate there to be 68 species.

Based on results obtained from morphological and molecular characters, Hagedorn & Scholler (1999) and Scholler et al (1999) proposed that nematode-trapping fungi should be organized in four genera: *Dactylellina* M. Morelet characterized by stalked adhesive knobs including species characterized by non-constricting rings and stalked adhesive knobs; *Gamsylella* M. Scholler, Hagedorn & A. Rubner characterized by adhesive branches and unstalked knobs; *Arthrobotrys* characterized by adhesive networks; and *Drechslerella* Subram. characterized by constricting rings. Li et al. (2005) emended genus *Gamsylella* and transferred species from *Gamsylella* to *Arthrobotrys* and *Dactylellina*. *Gamsylella* was not treated by them as a valid genus as proposed by Scholler et al. (1999). Yang & Liu (2006) later proposed to combine *Dactylellina* and *Gamsylella* into one genus based on molecular phylogenetic analyses. However, there are still debates concerning the generic concepts of *Gamsylella*.

The genus *Dactylellina* was described by Morelet (1968) with *Dactylellina leptospora* (Drechsler) M. Morelet as type species. Scholler et al. (1999) later transferred all predacious species forming adhesive stalked knobs and non-constricting trapping rings to this genus. Thirty-two names are listed for this genus in Index Fungorum (Index Fungorum, 2011). The current names for most species in the genus are in *Arthrobotrys* (1) *Dactylella* (3) *Gamsylella* (4) and *Monacrosporium* (8) and only seven species are listed under *Dactylellina* while the remaining are anamorphic *Orbilia* (Index Fungorum 2011)

Drechslerella was described by Subramanian (1964) based on the type species, *Drechslerella acrochaeta* (Drechsler) Subram. Scholler et al. (1999) later revised and transfered all predacious species forming constricting rings to this genus. Fourteen names are listed in this genus in Index Fungorum (Index Fungorum 2011), while Kirk et al. (2008) estimated there are one species. Species Fungorum (2011) currently lists seven names as anamorphic *Orbilia*, while the other species are organized in *Arthrobotrys* (3), *Dactylella* (1), *Geniculifera* (1) and *Monacrosporium* (3).

Gamsylella was described by Scholler et al. (1999) based on *G. arcuata* (Scheuer & J. Webster) M. Scholler, Hagedorn & A. Rubner Scholler et al. (1999) proposed *Gamsylella* as a new genus combining all predacious species that formed adhesive columns and unstalked knob devices to this genus. Li et al. (2005) later transferred those species to *Arthrobotrys* and Yang & Liu (2006) combined this genus with *Dactylellina* based on molecular phylogenetic analyses. Six taxa belonging to *Gamsylella* were reported by Index Fungorum (2008) and Kirk et al. (2008). Nevertheless, a placement of this genus based on phylogenetic analyses still remains in questioning and therefore it should be revaluated.

Dactylella was proposed by Grove (1884) based on the type species *Dactylella minuta* Grove a nematode-trapping species. The genus is characterized by erect, simple, hyaline conidiophores with conidia produced singly at the apex. Conidia are ellipsoidal, fusoid or cylindrical, one-celled at first and later having 2 to many septa. This genus has been emended several times and both non-predacious and predacious fungi have been included (Subramanian, 1963), Schenck et al. 1977; de Hoog & Oorschot, 1985; Zhang et al. 1994). Rubner (1996) revised the generic concept of *Dactylella* and excluded the nematode-trapping species. However, several nematode predacious species still remain in

Dactylella (Liu & Zhang 2003, Zhang et al. 2005). This genus was revisited by Liu & Zhang (2003) and was separated into three groups such as *Dactylella*, *Vermispora* and *Brachyphoris*. One hundred and eight *Dactylella* species are listed in Index Fungorum (Index Fungorum, 2011) where there are 62 estimated species (Kirk et al. 2008).

Phylogenetic significance and evolution of trapping devices

Morphology-based classification of fungi has been demonstrated to be inadequate in reflecting natural relationships among fungi. Phylogenetic analyses using molecular data, thus, have been used for more than a decade to assess phylogenetic relationships and also to revaluate the phylogenetic importance of various morphological characters (Cai et al. 2009). The first notable phylogeny study on nematode-trapping fungi was that of Rubner (1996). He used trapping devices to rationalize the classification of nematode-trapping fungi using molecular data. Later phylogenetic studies based rDNA sequence analysis also found that trapping devices are more informative than other morphological characters in delimiting genera (Liou & Tzean, 1997, Pfister 1997, Ahrén et al. 1998, Scholler et al. 1999, Ahrén & Tunlid 2003, Kano et al. 2004, Li et al. 2005, Yang & Liu 2006, Yang et al. 2007a, Liu et al. 2009). For example, Ahrén et al. (1998) revealed nematode-trapping fungi grouping in three lineages based on different types of trapping devices. Scholler et al. (2009) classified nematode-trapping fungi into four genera using 18S and ITS rDNA analysis. Li et al. (2005) re-evaluated the placement of nematode-trapping genera based 28S, 5.8S and β-tubulin analysis and the establishment of *Gamsylella* proposed by Scholler et al. (1999) was criticized and not accepted. Yang & Liu (2006) proposed to combine *Dactylellina* and *Gamsylella* into one genus and Yang et al. (2007b) traced the evolution of trapping devices in predatory fungi based on analyses of ITS, rpb2, ef-1, β-tubulin sequences. However, the morphological affinity of *Gamsylella* to genera *Arthrobotrys* and *Dactylellina* are still unclear and intergeneric relationships of *Gamsylella* and its allies are still unresolved.

The evolution of nematode-trapping devices has been discussed by Li et al. (2005) and Yang et al. (2007a). Phylogenetic analysis of nucleotide sequences demonstrated that early trapping structures evolved along two lines, yielding two distinct trapping mechanisms. One lineage developed into constricting rings and the other into adhesive traps. The adhesive network separated early. The adhesive knob evolved through stalk elongation, with a final development of nonconstricting rings. Li et al (2005) on the otherhand showed a conflicting result.

Orbiliales ITS and 28s rDNA-specific PCR primers which directly detect nematode-trapping fungi without culturing were developed by Smith & Jaffee (2009). The authors believe the combined use of Orbiliales-specific primers and culture-based techniques may benefit future studies of nematophagous fungi and can also be used to screen fungal isolates for phylogenetic placement in the Orbiliales.

Ancient nematode-trapping fungi

An early record of a nematode-trapping fungus is that of *Palaeoanellus dimorphus* which lived approximately 100 million years ago in a limnetic-terrestrial microhabitat (Schmidt et al. 2008). The fossil probably represents an anamorph of an ascomycete with unicellular hyphal rings as trapping devices and formed blastospores from which a yeast stage developed. The authors speculated that because predatory fungi with regular yeast stages are not known from modern ecosystems, the fungus is assumed to not be related to any recent nematode-trapping fungi and is probably an extinct lineage. Alternatively, it may be that we may yet find this strange species in modern settings.

Biodiversity of nematode-trapping fungi

Hawksworth (1991) estimated that there are 1.5 million global species of fungi and this has been accepted as a working figure by many mycologists. There have been several other publications debating estimates of fungal species (Hammond 1992, Cannon 1997, Huhndorf & Lodge 1997, Hyde et al. 2007). Nevertheless, however many fungi exist in nature, there are few (*ca* 100,000) that have been described. Hyde (2001) pointed out that most of the undescribed fungi are microfungi and they may occur in poorly investigated areas and less explored niches, substrates, hosts abd habitats.

There has been a relatively large numbers of studies on fungal diversity such as in extreme environments (Connell et al. 2006, 2008, Fell et al. 2006, Porras-Alfaro et al. 2008), in marine habitats (Hyde 1996, Poon & Hyde 1998, Barata 2006, Hyde & Sarma 2006, Lai et al. 2007, Laurin et al. 2008, Nambiar et al. 2008), in freshwater habitats (Tsui et al. 2000, Cai et al. 2003, Fryar et al. 2004, Tsui & Hyde 2004, Duarte et al. 2006, Sole et al. 2008), in terrestrial habitats (Hyde & Alias 2000, Sun & Liu 2008, Wakelin et al. 2008a), in areas of environmental pollution (Indra & Meiyalagan 2005, Zafar & Ahmad 2005, Ellis et al., 2007, Duarte et al. 2008, Stefanowicz et al. 2008, Turnau et al. 2008), on decaying litter (Tsui et al. 2000, Cai et al. 2003, Tsui & Hyde 2004, Gulis et al. 2008, Lonsdale et al. 2008). However, there are relatively few diversity studies of nematode-trapping fungi (Hao et al. 2005, Mo et al. 2006, 2008, Saxena 2008). Hao et al. (2005) studied the diversity of nematode-trapping from aquatic habitats; Mo et al. (2006, 2008) studied diversity of nematode-trapping fungi from heavy metal polluted soils. Interestingly, Mo et al. (2008) revealed that the diversity index of nematode-trapping fungi was positively correlated with concentration of heavy metals.

Diversity study on nematode-trapping fungi using traditional methods has involved in several processes, such as sample collection, isolating with nematodes, preliminary morphological examination of fungal structures, single spore isolations for examining trapping devices and identifying species. These methods have been commonly used because of their low cost and the fact that they are easy to conduct (Jeewon & Hyde, 2007). The traditional methods used in nematode-trapping fungi largely rely on the discovery of fungal spores in natural environments. Hyde & Goh (1998) pointed out that the incubation of substrates effects the structure of fungal communities recorded. Jeewon & Hyde (2007) suggested that a large number of fungi existing as mycelial propagules or dormant spores and can be numerically dominant populations but in their natural environment they may have little functionality.

Molecular techniques have been used to investigate fungal diversity. The emergence of these molecular methods overcomes the limitations associated with traditional approaches and isolation based methods. Jeewon & Hyde (2007) recently reviewed advance molecular techniques versus traditional techniques that are used in the detection and diversity of fungi from environmental samples. Molecular methods used in assessing fungal diversity have been employed such as Denaturing Gradient Gel Electrophoresis (DGGE), Terminal Restriction Fragment Length Polymorphism (T-RFLP), Amplified rDNA Restriction Analyses (ARDRA), Amplified Random Intergeneric Spacer Analysis (ARISA), and Temperature Gradient Gel Electrophoresis (TGGE). Recently PCR-based fingerprinting techniques have been applied to assess fungal diversity. Oligonucleotide Fingerprinting of Ribosomal RNA Gene (ORFG), a new method that sorts arrayed rRNAgene clones into taxonomic clusters through a series of hybridization experiments (Kirk et al. 2004). Most frequently used methods in assessing fungal diversity are Denaturing Gradient Gel Electrophoresis (DGGE) and Terminal Restriction Fragment Length Polymorphism (T-RFLP). Wakelin et al. (2008b) used a semi-quantitative nested quantitative PCR approach and a DGGE approach to detect soil total *Fusarium* communities on maize root. Li et al. (2008) used a combination of plate count, DGGE and clone library analyses to investigate the effect of methamidophos on soil fungi community in microcosms. Raberg et al. (2005) used T-RELP to detect the early stages of wood decay and this was compared with microscopic evaluation. Yet, there is no study on diversity of nematode-trapping fungi using molecular methods.

Although traditional methods and molecular based methods both have disadvantages and advantages, traditional methods presently still have some advantages over molecular based techniques in assessing fungal diversity. Most of the molecular techniques involved do not discriminate between active and inactive stages of fungi (Jeewon & Hyde, 2007). Data yielded from molecular techniques are difficult to employ with respect to ecology and function (e.g. correlation analysis between environmental factors and fungal communities). Moreover, traditional methods often involve less cost and no expensive specialized laboratory

equipment is needed, which are often not available in developing world. In contrast, current knowledge on the diversity and detection and the community structure of the nematode-trapping fungi in nature is still rudimentary. Improvement in traditional approaches combined with molecular techniques will provide a better understanding of these fungal community systems in nature.

Ecology, occurrence and geographical distribution

There have been numerous surveys on the occurrence of nematophagous fungi, which have shown that the fungi are found throughout the world and in all types of climate and habitats (Duddington 1951, 1954, Gray 1987, Sunder & Lysek 1988, Boag & Lopez-Llorca 1989, Saxena & Mukerji 1991, Dackman et al. 1992, Liu et al. 1992, Saxena & Lysek 1993, Rubner 1994, Persmark & Nordbring-Hertz 1997, Persmark & Jansson 1997, Jaffee 2003, Ahrén et al. 2004, Hao et al. 2005, Jaffee & Strong 2005, Farrell et al. 2006, Su et al. 2007, Mo et al. 2008, Saxena 2008). The teleomorph state *Orbilia* of nematode-trapping fungi have been recorded on decaying wood from terrestrial and freshwater habitats (Pfister 1994, Webster et al. 1998, Liu et al. 2005, 2006, Zhang et al. 2006, 2007, Yu et al. 2007), and the anamorphic states also commonly occur in terrestrial, freshwater and marine habitats (Hao et al. 2004, Li et al. 2006, Swe et al. 2008a, b, 2009), but rarely occur in extreme environments (Onofri & Tosi 1992). There have been several studies on nematode-trapping fungi because of their potential in biological control, however most of these have concentrated on agriculture and animal husbandry or forestry (Kerry & Hominick 2002, Ahrén & Tunlid 2003, Jaffee & Strong 2005, Dong & Zhang 2006, Su et al. 2007) or freshwater environments (Maslen 1982, Hao et al. 2005). Numerous fungal-animal associa-tions have been reported from aquatic habitats. The first report of marine predacious fungi was three zoophagous forms discovered in brackish water (Jones 1958). Currently, more than 50 species of predacious hyphomycetes have been recorded from aquatic habitats (Ingold 1944, Peach 1950, 1952, Johnson & Autery 1961, Anastasiou 1964, Hao et al. 2004, 2005). *Arthrobotrys dactyloides* Drechsler was the first species of nematode-trapping fungi to be reported from brackish water (Johnson & Autery 1961) while Swe et al. (2008a, b, 2009) recorded several species from mangroves.

Factors affecting the distribution of nematode-trapping fungi

The distribution and occurrence of nematode-trapping species and groups of fungi is associated with specific soil variables in particular pH, moisture, nutrients (N, P, K), heavy metal and nematode density (Gray 1985, Persson & Baath 1992, Jaffee 2004b, Sánchez-Moreno et al. 2008, Mo et al. 2008). Gray (1988) revealed that soil nutrients such as N, P and K were all positively correlated with nematode density. Species with stalked knobbed trapping devices (*Dactylellina*) and those species with constricting rings (*Drechslerella*) were isolated more readily from richer soils which contained a greater density of nematodes. However, net-forming species (*Arthrobotrys*) are largely independent of soil fertility, especially low K (Burges & Raw 1967). Interestingly, Mo et al. (2008) found that diversity of nematode-trapping was positively correlated with lead concentration. These soil variables are known to vary with depth, as are the densities of soil bacteria, fungi and nematodes (Mankau & McKenny, 1976, McSorley et al. 2006) and a high level of nematode-trapping activity have been recorded from the rhizosphere area (Peterson & Katznelson 1964, Mitsui et al. 1976, Persmark & Jansson 1997, Wang et al. 2003, McSorley et al. 2006). However, there are large variations depending on plant and soil types (Jansson & Lopez-Llorca 2001). The species of nematode-trapping fungi vary with depth (Gray & Bailey 1985). Peterson & Katznelson (1964) revealed that the greatest diversity occurred in the upper 10–30 cm of soils, and this was a positive correlation between the population density of nematophagous fungi and root-knot nematodes in peanut fields. Gray & Bailey (1985) have examined the vertical distribution of nematophagous fungi in soil cores collected from a deciduous woodland, predators forming constricting rings, adhesive branches and adhesive knobs are restricted to the upper litter and humus layer, while the net-forming predators and endoparasites were isolated at all depths, although they are significantly more abundant

in the lower mineral-rich soils. In contrast, predators able to form traps spontaneously are restricted to the organic soils of the hemi-edaphic zone which are rich in nematodes. Nematophagous fungi are small enough to be affected by micro-climates within the soil (Gray 1985). Hao et al. (2005) observed that the nematode-trapping were not detected deeper than four meter in a freshwater pond. Several studies have also been carried out on horizontal distribution (Persson et al. 2000, Segers et al. 2000, Minglian et al. 2004). For example, Persson et al. (2000) studied the growth and dispersion of *Arthrobotrys superba* Corda under natural conditions determined by a radioactive tracing technique.

The effect of major biotic and abiotic variables such as soil moisture, organic matter, pH, nematode density, soil nutrients (Gray 1987) and submerged water condition on the distribution of nematode-trapping fungi has been extensively studied. The diversity was highest at the depth of 20 cm and no nematode-trapping fungi were found at the depth of 4 m (Hao et al. 2005). Heavy metals concentrations affected distribution of NTF and was not negatively affected by Pb concentration (Mo et al. 2006, Mo et al. 2008). However, treatment with ethylenediamine tetra-acetic acid (EDTA) resulted in detecting various stages of fungi of aggregates in the sediments from -5000 m deep sea, gradually revealing the presence of fungal hyphae within them (Damare & Raghukumar 2008). Gray (1987) pointed out that the endo-parasitic nematophagous fungi are obligate parasites, and unlike the predatory fungi, they appear to be unable to live as saprotrophs in the soil. He also suggested that non-specific method of attraction may rely on a greater density of soil nematodes to ensure infection, as compared with parasites which produce adhesive conidia (Gray 1987).

Gray (1988) revealed that soil nutrients N, P and K were all positively correlated with nematode density. Based on his results, knob-forming predators which rely on their ability to produce traps spontaneously are isolated from soils with low concentration of nutrients, while those species with constricting rings are isolated from richer soils which contain a greater density of nematodes. Net-forming species are largely independent of soil fertility, although generally they are isolated from soils with limited nutrients, especially low K (Burges & Raw 1967).

Effect of salinity

The effect of salinity on fungal growth in yeasts and moulds (Blomberg & Adler 1993, Dan et al. 2002), marine fungi, mycorrhizal fungi and some wood-rotting basidiomycetes has been studied (Ritchie 1959, Davidson 1974, Byrne & Jones 1975, Jones & Byrne 1976, Kohlmeyer & Kohlmeyer 1979, Siegel & Siegel 1980, Hyde et al. 1987, Lorenz & Molitoris 1992, Clipson & Hooley 1995, Akira & Tadayoshi 1996, Castillo & Demoulin 1997, Juniper & Abbott 2006, Sharifi et al. 2007). Some research has studied the effects of salinity on the growth and the parasitic ability of the parasitic fungi, with most having studied the parasites of mosquitoes (Harrison & Jones 1971, Lord & Roberts 1985, Gardner & Pillai 1986, Lord et al. 1988, Kramer 1990, Teng et al. 2005). The effect of abiotic factors, such as temperature, pH, light, UV and nutrition on the trapping efficacy of nematode-trapping fungi has been intensively studied (Ciordia & Bizzell 1963, Gray 1985, 1988, Morgan et al. 1997, Fernandez et al. 1999, Gronvold et al. 1999, Zucconi et al. 2002, Jaffee 2006, Kumar & Singh 2006a, 2006b, Paraud et al. 2006, Sun & Liu 2006, Gao et al. 2007).

Ecological speciation

Speciation, the evolution of one species into two, is one of the most fundamental problems to appreciate in biology (Giraud et al. 2008). Numerous reviews on the modes of speciation in fungi have been published (Natvig & May 1996, Burnett 2003, Kohn 2005, Giraud et al. 2008). 'Ecological speciation', as defined by Rundle & Nosil (2005) is '*the process by which barriers to gene flow evolve between populations as a result of ecologically based divergent selection'*. Fungi are excellent models for the study of eukaryotic speciation in general (Burnett 2003, Kohn 2005). However, they are still rarely included in general reviews on this subject. Giraud et al. (2008) explained why fungi is a excellent models for studying speciation; (1) Many fungi can be cultured *in vitro* and many experiments on mating types among fungal species have been reported, (2)

Fungi display a huge variety of life cycle and geographical and ecological distributions, allowing the study of parameters most significantly influencing the speciation processes, (3) Numerous species complexes are known in fungi, encompassing multiple recently diverged sibling species which allows investigations on the early stages of speciation.

It is important to define a species before studying speciation. The traditional species concept is the morphological species concept (MSC) and in fungi is mainly based on morphology and reproductive behavior (Taylor et al. 2000). On the other hand, some mycologists have debated that species concepts should also be considered on an ecological basis as well as on nucleotide divergence (ESC, ecological species concept and phylogenetic species concept, PSC) (Harrington & Rizzo 1999). Nevertheless, the most commonly used species criterion for the fungi has been the morphological species concept. However, many cryptic species have been discovered within morphological species, using the biological species concept (e.g. Anderson & Ullrich 1979) or the genealogical goncordance phylogenetic species recognition, GCPSR (Taylor et al. 2000). Moreover, the phylogenetic species concept uses the phylogenetic concordance of multiple unlinked genes to indicate a lack of genetic exchange and thus evolutionary independence of lineages. Thus, species can be identified which cannot be recognized using other species criteria due to the lack of morphological characters (Giraud et al. 2008). Recently, the genealogical concordance phylogenetic species recognition criterion is also useful tool or criterion in fungi and is most widely used within the fungal kingdom (Johnson et al. 2005, Pringle et al. 2005, Le Gac et al. 2007).

Knowing which genes are involved in reproductive isolation may help to get a better understanding of speciation processes (Giraud et al. 2008). There has been little research to understand the genetics of speciation in fungi. Four of five genes were involved in the intersterility among *Heterobasidion* species (Chase & Ullrich 1990). DNA multi-locus typing showed that different clones of the fungus are associated with different environments (Fisher et al. 2005), which indicated that adaptation to new environments constrains the organism's ability to successfully disperse in nature. The population structure in asexual parasites may reflect host or habitat adaptation at all loci, because selection at one locus results in hitchhiking of the whole gene (Giraud et al. 2008)

'The ecological species concept (ESC)' and 'ecological speciation' have been proposed as an important component of speciation among widely spread and diverse living organisms such as fish (Hatfield &Schluter 1999), lizards (Ogden & Thorpe 2002, Richmond & Reeder 2002), and insects (Via 1999, Via et al. 2000, Rundle & Nosil 2005, Barat et al. 2008). There have been some studies on host speciation in fungi (Antonovics et al. 2002, Couch et al. 2005, Lopez-Villavicencio et al. 2005). However, ecological speciation in fungi has not received much attention. One of the first studies on ecological speciation was on the insect pathogenic fungi, *Metarhzium anisoplaie* by Bidochka et al. (2001) and in their study *M. anisoplaie* clearly separated into two genetic groups based on two habitats; agriculture and forest. Another study was on a plant pathogen of grasses, *Claviceps purpurea* and the result shown that terrestrial isolates were significantly divergent from other isolates of wet /shady and salt marsh habitats (Douhan et al. 2008). There have however, been few related studies on nematode-trapping fungi. Geographical speciation among 22 isolate of *Duddingtonia flagrans* (Dudd.) R.C. Cooke suggested that there was no or little genetic variation (Ahrén et al. 2004). However, using selective fragment length amplification, Mukhopad hyaya et al. (2004) found that *D. flagrans* isolates are genetically diverse despite their morphological similarities.

Fungal-nematode interactions

Host recognition, adhesion, host specificity and infection process

Nematophagous fungi are an important group of soil microorganisms that can suppress the populations of plant and animal parasitic nematodes. They can be grouped into three categories according to their mode of infestation: nematode-trapping, endoparasitic, and toxic compound producing (Nordbring Hertz & Tunlid 2000). The pathogenic mechanisms

during the infestation process are diverse. They can be mechanical through the production of specialized capturing devices, or through production of toxins that kill nematodes. During infection, a variety of virulence factors may be involved against nematodes by nematophagous fungi. The infection processes and host range of nematophagous fungi have been studied using various techniques such as light and low temperature electron microscopy and bioassays and have been supported by biochemical, physiological, immunological and molecular techniques (Thorn & Barron 1984, Murray & Wharton 1990, Jansson et al. 2000). The ultrastructure of the nematode-trapping devices has been extensively studied (Heintz & Pramer 1972, Nordbring-Hertz & Stalhammar-Carlemalm 1978, Dijksterhuis et al. 1994). The mode of infection by nematophagous fungi has been reviewed by Yang et al. (2007c).

Research on attraction of nematodes to fungi has focused on the host-finding behavior of fungal-feeding nematodes (Bordallo et al. 2002, Wang et al. 2010). Nematophagous fungi are attracted to plant and animal parasitic nematodes and microbivorous nematodes (Balan & Gerber 1972, Jansson & Nordbring-Hertz 1979, 1980). Zuckerman & Jansson (1984) review nematode chemotaxis and possible mechanisms of host/prey recognition. The attracttion of nematodes to nematophagous fungi has been studied using culture filtrates and macerated mycelium (Jansson & Nordbring-Hertz 1979) as well as living fungi (Jansson & Nordbring-Hertz 1980). One of the earliest observations described the attraction of the plant parasitic nematode *Meloidogyne incognita* to tomato roots grown in sterile Petri plates (Zuckerman & Jansson 1984). *Penagellus redivivus* was attracted to approximately 75% of the mycelium of nematophagous fungi tested (Kuyama & Pramer 1962, Nordbring-Hertz 1973, Barron 1977, Jansson 1982). Fungal feeding and plant parasitic nematodes seem to respond differently to fungal chemotactic factors (Ward 1973, Field & Webster 1977, Zuckerman & Jansson 1984, Zhao et al. 2007), e.g. fungal feeding nematodes were attracted to all fungi tested, while some plant parasitic nematodes were attracted to very few fungi (Field & Webster 1977); the volatiles produced by the host plants could be the basis of a chemoecological relationship between plant parasitic nematodes and their vector insects (Zhao et al. 2007). Jansson (1982) showed that the presence of trapping devices on the hyphae increases the ability of fungi to attract nematodes. Trapping devices could be produced spontaneously, or their formation can be induced by nematodes or proteinaceous compounds (Jansson & Nordbring-Hertz 1979). The connection between attraction ability and degree of parasitism was also confirmed when the parasitic ability of the fungi was tested in soil microcosms (Tunlid et al. 1992, Dijksterhuis et al. 1994).

More recently, Wang et al. (2009) investtigated the attraction of *Esteya vermicola* J.Y. Liou, J.Y. Shih & Tzean to the pinewood nematode. The endoparasitic fungus was attracted to living mycelia and exudative substances of *E. vermicola* reflecting the dependence of the fungi on nematodes for nutrients. Attractive substances appeared to be avolatile exudatives and volatile diffusing compounds.

Adhesion to host is an essential requirement for fungal parasites to be able to infect. Most of pathogenic and parasitic fungi, adhesion is mediated by an extracellular matrix (ECM) or sheath on the fungus (O'Connell 1991, Åhman et al. 2002, Alston et al. 2005). Tunlid et al. (1992) suggested that extracellular adhesions are produced on the surfaces of spores, appressoria and trapping devices and are essential for infection. The adhesive layer has a fibrillar structure with residues of neutral sugars, uronic acid and proteins (Whipps & Lumsden 2001). Jansson & Lopez-Llorca (2001) suggested that the adhesion process is much more complicated than a simple receptor-ligand binding, and may involve the activity of the fungal infection structure as well as the surface of living nematodes. Initial contact with the host cuticle may be followed by interactions with specific receptors, reorganization of surface polymers to strengthen the adhesions, changes in morphology and the secretion of specific enzymes (Jansson & Nordbring-Hertz 1988, Kerry 2000, Abiko et al. 2005). These processes and the structures involved have been extensively reviewed (Kerry et al. 1993).

Extracellular enzymes involved in nematode infestation process

During the infection process, the cuticle must be penetrated, the nematode is immobilized, and the prey is finally invaded and digested. This sequence of infection seems to be present in most nematophagous fungi, but the molecular mechanisms are not well understood (Lopez-Llorca & Duncan 1988, Dackman et al. 1989). However, several nematophagous fungi have been reported to produce nematotoxins that immobilize or kill nematodes, and ultrastructural and histochemical studies suggest that the penetration of the nematode cuticle involves the activity of hydrolytic enzymes (Schenck et al. 1980). Enzymes involved in the infection processes of nematophagous fungi are being cloned and characterized. Also, many scientists have performed screens of nematophagous fungi in order to identify the structures of compounds produced in vitro that may have nematicidal action. There is a recent review on the modes of infection and the biochemical properties of the serine proteases enzyme (Yang et al. 2007c).

Studies of insect and other parasitic fungi have shown that the chemical composition of the surface of the host is important for the hydrolytic enzymes involved in infection (Sahai & Manocha 1993). More detailed studies on *Metarhizium anisopliae* (Metschn.) Sorokīn has shown that proteases are produced more rapidly and in higher concentrations than other cuticle-degrading enzymes (Goettel et al. 1989, Veenhuis et al. 1985). There is much evidence related to protease and chitinase production by entomophagous fungi (Jansson & Friman 2000, Tikhonov et al. 2002). Proteases are the only enzymes produced in large amounts (Maher 1993). Furthermore, the protein coating of chitin microfibrils in extracellular barriers of insects and nematodes would render microibrils relatively non-amenable to enzymolysis (Rong De et al. 2005). It can therefore be assumed that the activity of proteases is more important than chitinase in host penetration. However, the importance and function of extracellular proteases in the infection process between nematodes and fungi are still unknown.

The first study on proteases and their involvement in the infection and immobilization of nematodes by the nematode-trapping fungi, *Arthrobotrys oligospora* was by Tunlid & Jansson (1991). Subsequently, a first pathogenic serine protease (P32) from the nematode egg parasite *Verticillium suchlasporium* W. Gams & Dackman was purified and characterized by Lopez-Llorca & Robertson (1992). Recently more pathogenic serine proteases were detected, characterized, and cloned by several scientists, for examples Aoz1 from *Arthrobotrys oligospora* (Zhao et al. 2005), M1x from *Monacrosporium microscaphoides* Xing Z. Liu & B.S. Lu (Wang et al. 2006a), and Ds1 from *Dactylella shizishanna* X.F. Liu & K.Q. Zhang (Wang et al. 2006b), Ac1 from *Arthrobotrys conoides* Drechsler (Yang et al. 2007b), and Dv1 from *Dactylellina varietas* Yan Li, K.D. Hyde & K.Q. Zhang (Yang et al. 2007c). There have been some research on chitinase and other hydrolytic enzymes produced by nematode-trapping fungi. Lipases, amylases and pectinases have been detected *in vitro* in egg parasites fungi (Lopez-Llorca & Duncan 1988, Dackman et al. 1989). Collagenase was isolated from *Arthrobotrys amerospora* S. Schenck, W.B. Kendr. & Pramer (Tosi et al. 2002) and an extracellular chitinase CHI43 from *Pochonia chlamydosporia* (Goddard) Zare & W. Gams and *P. suchlasporium* (W. Gams & Dackman) Zare & W. Gams (Lysek & Krajci 1987). Acid phosphatase has been reported at the site of contact between nematodes and *A. oligospora* using ultrastructural techniques (Veenhuis et al. 1985). Acid and alkaline phosphatase activities have also been found in the ECM of *Drechmeria coniospora* (Drechsler) W. Gams & H.B. Jansson conidia (Jansson & Friman 2000). Maher (1993) suggested that phosphatase could be involved in adhesion.

Biological control of nematodes

Nematode-trapping fungi have long been considered promising biological agents for control of plant-parasitic nematodes (Dupon nois et al. 2001, Sorbo et al. 2003, Singh et al. 2007, Thakur & Devi 2007) and animal parasitic nematodes (Bogus et al. 2005, Mendoza-De Gives et al. 2006, Paraud et al. 2007, Carvalho et al. 2009, Santurio et al. 2011).

Use of NTF to control animal gut nematodes

Alternatives to using anthelmintic drugs for the treatment of nematode infections of various animals have been necessary because development of drug resistance nematodes (Carvalho et al. 2009, Santurio et al. 2011). The nematode-trapping fungus *Duddingtonia flagrans* (Dudd.) R.C. Cooke has become an important organism in various integrated control strategies (Carvalho et al. 2009, Maciel et al. 2010, Santurio et al. 2011). Several studies have demonstrated that when chlamydospores of this nematode-trapping fungus are administered to sheep and other animals (e.g. dogs, cattle) there is a dramatic reduction of eggs of this nematode passed out in the faeces (Dias et al. 2007, Carvalho et al. 2009, Maciel et al. 2010, Santurio et al. 2011). It is unlikely that *D. flagrans* can be the cure-all for nematode parasite control of livestock or other animals, but it has potential for use in integrated control strategies (Maciel et al. 2010, Santurio et al. 2011).

Horses are also hosts to a wide variety of nematodes (Tavela et al. 2011). The viability of the nematode-trapping fungus *Monacrosporium thaumasium* (Drechsler) de Hoog & Oorschot 1985 administered in a formulation (pellets) against Cyathostomin nematodes was assessed in biological control of horses (Tavela et al. 2011). There was a significant reduction in egg counts in faeces following treatment, however, this did not significantly affect weight gains in the horses. It was therefore speculated that treatment of horses with pellets containing *M. thaumasium* may be effective in controlling cyathostomin (Braga et al. 2009, Tavela et al. 2011).

Use of NTF in traditional or natural biocontrol of plant nematodes

There has been great promise and much research in the use of nematode-trapping fungi for the biocontrol of nematodes (Khan et al. 2006, Soares et al, 2006). In one example Aboul-Eid et al. (2006) tested the commercial bio-product Dbx 1003 20% containing the nematode-trapping fungus *Dactylaria brochopaga* Drechsler against root-knot nematode *Meloidogyne incognita* infesting grapevine. There was a significant reduction of *M. incognita* in soil and in the number of root galls when comparing treated to untreated soils. The topic has been reviewed extensively (Martin & Zhang 2002, Khan et al. 2006, Mennan et al. 2006, Soares et al. 2006, Zhu et al. 2006) and is not discussed further here.

Studies to create favorable conditions for the NTF that naturally occur in the soil, to control nematode populations, have also been carried out (Duponnois et al. 2001, Jaffee 2004a, Sun & Liu 2006, Radwan et al. 2007). However, Cooke (1968) has revealed that the chance of establishing an 'alien' species of nematophagous fungi in the soil is small. Based on this Gray (1984) suggested that fungi are generally poor saprobic competitors in soil habitats, and are susceptible to antagonism from other soil organisms. Moreover, one of the major constraints to biological control is the inconsistency in efficacy which is often observed when useful antagonists reach the stage of large-scale glasshouse or field testing (Kerry & Hominick 2002). This can arise from a variety of causes reflecting the biological nature of the control microorganism (Hay et al. 1997, Bird et al. 1998). Therefore the use of NTF as biological control agents has not been hugely successful to date.

Using advance techniques

Nematophagous fungi are soil-living fungi that are used as biological control agents of plants and animal parasitic nematodes (Jansson et al. 1997). Direct applications to the soil using these agents may have little to no effect on the target nematodes. Their potential could be improved by genetic engineering, but the lack of information about the molecular background of the infection has precluded this development. Åhman et al. (2002) suggested that a way to improve the biocontrol potential of nematophagous fungi could be to increase the expression of the pathogenicity-related proteases. With the development of molecular techniques, increasing attention has been paid to understanding the molecular aspect of the infection process and identifying the potential virulence factors. Relatively high numbers of pathogenic serine proteases have been identified from nematophagous fungi and have been characterized and cloned. Moreover, to achieve successful control of parasitic nematodes using nematode-trapping fungi, a detailed knowledge

on the infection process is needed, for example, virulence factors have been identified and factors controlling their activity have been characterized (Åhman et al. 1996, Rosen et al. 1997). A transformation system also has to be developed to examine the function of virulence factors in detail, e.g., by constructing over expressing strains and knock-out mutants (Tunlid et al. 1999). Δ*PII* mutant was constructed in *Arthrobotrys oligospora* by homologous recombination (Åhman et al. 2002). However, the pathogenicity of the mutant was reduced only a little and it was suggested that there might be a significant residual proteolysis activity in the Δ*PII* mutant (Yang et al. 2007c). Åhman et al. (2002) suggested that genetic engineering can be used to improve the pathogenicity of a nematode-trapping species. In their study, the mutants containing additional copies of the PII gene developed a higher number of infection structures and had an increased speed of capturing and killing nematodes compared to the wild type.

Recently some advance techniques were developed such as the green fluorescent protein (GFP) and suppression subtractive hybridization (SSH), to study the interaction between the NTF and the nematodes. Ahrén et al. (2005) compared the gene expression patterns in traps and in the mycelium of the nematode-trapping fungus *Monacrosporium haptotylum* (Drechs ler) Xing Z. Liu & K.Q. Zhang by microarray analysis. The ability of a nematode-trapping fungus to become established in field soil is an important characteristic when considering its use as a biological control agent. Persson et al. (2000) determined the nematode-trapping fungus, *Arthrobotrys superba* in the soil using a radioactive tracing method. PCR is becoming an important tool in fungi not only for its original use (nucleic acid amplification), but also for gene cloning, the specific study of genes involved in pathogenesis (Goller et al. 1998).

Commercialization of products

The goal of biocontrol research using nematophagous fungi is to provide additional tools for nematode management and to deliver these tools to growers, therefore products must be commercialized. There have been relatively few successes in developing commercially acceptable formulations of nematophagous fungi. In most cases, fungi have been mass produced on solid substrates such as cereal grain or bran and the colonized substrate has been applied to the soil. Formulations based on alginate (Kerry et al. 1993, Jaffee & Muldoon 1995) and other materials, have been produced on a limited scale, but the submerged fermentation and downstream processing technologies currently used for production of biological herbicides, have never been used. In two companion paper, Stirling et al. (1998a, b) reported attempts to mass produce both egg-parasitic and nematode-trapping fungi in submerged culture and convert the fungal biomass into a granular product suitable for commercial use. Biologically active kaolin based formulations of *Verticillium chlamydosporium* were produced that parasitized eggs of the root-knot nematode *Meloidogyne javanica* in glasshouse tests (Stirling et al. 1998a). Similar formulations of *Arthrobotrys dactyloides* Drechsler reduced the number of juveniles in soil microcosms and numbers of galls on roots of plants grown in the glasshouse (Stirling et al. 1998b). A number of the formulated products have been tested in the field and green house (Jaffee & Muldoon, 1995, Waller et al. 2001; Araujo et al. 2004b) and the predatory activity of nematode-trapping fungi has been screened for use as biological control agents (Araujo et al. 1996, Araujo et al. 2004a). However, the development of fungal biological control agents for commercial use may be limited by several factors. e.g chemical, physical, and abiotic factors in the soil would influence the growth of fungi (Mo et al. 2005).

It is clear that the commercialization of these microorganisms lags far behind the resource investigation. One limiting factor is their inconsistent performance in the field, due to virulence loss and insufficient quality control in pre-application steps. With the help of advance techniques (e.g. genomics, crystallography, and the suppression subtractive hybridization methods), we may obtain clear understanding on the encoding genes of traps, the signaling pathways that control the switch from saprotrophy to parasitism, and the molecular mechanism of the infection process (Yang et al. 2007c). Such information will provide a novel approach to improve the efficacy of nematode-

trapping fungi for biological control of nematode pests.

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