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**Review**

# Nematophagous Fungi - Classification, Ecological Roles, and Their Potential in Biocontrol of Nematode Parasite

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## Abstract

*Nematophagous fungi are specialized microorganisms that thrive in nitrogen-poor soils by preying on or parasitizing nematodes. With over 700 species spanning various phyla, these fungi are categorized into nematode-trapping/predatory, endoparasitic, and egg- and cyst-parasitic groups. Nematode-trapping fungi utilize diverse mechanisms, such as adhesive hyphae and constricting rings, to capture and digest nematodes. Endoparasitic fungi infect nematodes internally via spores, while egg- and female-parasitic fungi target nematode eggs and sedentary females with appressoria or zoospores. As biocontrol agents, these fungi offer an eco-friendly alternative to chemical pesticides by either directly introducing them into the soil or enhancing native fungal activity. Successful applications in controlling both plant and animal nematodes, including the use of Duddingtonia flagrans and Pochonia chlamydosporia, demonstrate their potential for sustainable nematode management.*

**Keywords:** Biocontrol Agents, Fungal Parasitism, Nematophagous Fungi, Nematode Biocontrol.

# Introduction

## Nematophagous Fungi

Predatory fungi are natural enemies of many nematode groups and therefore exhibit low host specificity. Typically, predatory fungi are saprophytes that become predators under certain conditions to capture live, vermiform nematodes (Lopez-Llorca and Jansson, 2007). Carnivorous nematophagous fungi, thriving in nitrogen-poor soils, derive nutrients by preying on or parasitizing nematodes. These fungi utilize specialized traps to capture prey, hyphae tips to parasitize nematode females and eggs, and conidia that adhere to nematodes while producing toxins to attack them (Abd-Elgawad *et al*., 2018). In most studies, nematophagous fungi are administered by feeding cultured grain or as sodium alginate pellets. The spores become active and attack parasitic larvae only after passing through the gastrointestinal tract (GIT) of the host animal and being excreted with the feces. Therefore, adverse effects on the animal are not anticipated (Burke and Miller, 2020).

There are currently more than 700 described species of nematophagous fungi (NFs), spanning several phyla, including *Ascomycota*, *Oomycota*, *Basidiomycota*, *Chytridiomycota*, and *Zygomycota* (Hsueh *et al*., 2017; de Freitas Soares *et al*., 2018). Nematophagous fungi are classified into three main groups: (1) nematode-trapping/predatory fungi; (2) endoparasitic fungi; and (3) egg- and cyst-parasitic fungi (Lopez-Llorca *et al*., 2008). Generally, nematode-trapping and egg- and cyst-parasitic nematophagous fungi can also survive saprophytically, whereas endoparasitic nematophagous fungi must use nematodes to complete their development (de Freitas Soares *et al*., 2018).

Nematodes are motile, and nematophagous fungi utilize specialized traps or toxins to capture them (Zhang *et al*., 2016). Predatory fungi, the most common type found in nature, produce modified hyphae called traps to bind and digest nematode prey (de Freitas Soares *et al*., 2018). After brief contact with nematodes, the fungal mycelia spontaneously differentiate into functional structures (traps) that adhere to, penetrate, kill, and digest the nematodes' contents (Yang *et al*., 2007). These traps include non-differentiated adhesive hyphae, three-dimensional adhesive networks, adhesive nodules, and constricting and non-constricting rings (de Freitas Soares *et al*., 2018).

A notable feature of nematode-trapping fungi is their ability to detect the presence of prey using cues such as pheromones (Hsueh *et al*., 2013), peptides, and nematode extracts (Zhang *et al*., 2016). This review focuses on some of the most effective nematophagous fungi for classification, ecological roles, and their potential in the biocontrol of nematode parasites.

## Classification of Nematophagous Fungi

### *Nematode-Trapping/Predators*

Nematode-trapping fungi are a fascinating and distinctive group of carnivorous microorganisms that use specialized structures to ensnare and digest nematodes. These fungi can create various trapping mechanisms, such as adhesive hyphae, adhesive knobs, adhesive networks, constricting rings, and non-constricting rings. Found in regions worldwide from the tropics to Antarctica and in both terrestrial and aquatic ecosystems these fungi play a vital ecological role in controlling nematode populations in soil (Jiang *et al*., 2016). The most important genera include *Purpureocillium, Pochonia, Hirsutella, Nematophthora, Arthrobotrys, Drechmeria, Fusarium,* and *Dactylellina* (Siddiqui and Mahmood, 2016). Among these nematophagous fungi, only a few species are obligate parasites of nematodes, while the majority are facultative saprophytes (Zhang *et al*., 2016).

Nematode-trapping fungi are soil-dwelling fungi that capture free-living nematodes using specialized trapping structures. These fungi have developed advanced trapping mechanisms, including constricting rings and five types of adhesive traps: sessile adhesive knobs, stalked adhesive knobs, adhesive nets, adhesive columns, and non-constricting rings (Su *et al*., 2017). Approximately 380 species of nematode-trapping fungi have been identified globally (Zhang *et al*., 2011). Different fungal species can produce one or more types of these trapping devices (Yang *et al*., 2007). Most nematode-trapping fungi can live both saprophytically on organic matter and as predators by capturing small animals. Traps serve not only as weapons for attacking nematodes but also as indicators of the fungi's transition from a saprophytic to a predatory lifestyle (Li *et al*., 2011).

Nematode-trapping fungi are generally not host-specific and can trap all soil-dwelling nematodes (Nordbring-Hertz *et al*., 2006). These fungi are classified into four genera: *Arthrobotrys* (adhesive three-dimensional networks), *Dactylellina* (stalked adhesive knobs and/or non-constricting rings), *Drechslerella* (constricting rings), and *Gamsylella* (adhesive branches and unstalked knobs). However, due to new nomenclatural regulations that require only one name per fungus, the names of these nematode-trapping fungi need to be revised (Hawksworth *et al*., 2011).

### *Endo-Parasitic (Endozoic) Fungi*

Endoparasitic fungi are a category of nematophagous fungi that infect nematodes by producing spores. These spores can be internalized by nematodes through ingestion or attach to the nematode epidermis, initiating infection (Liu *et al*., 2009). Endoparasitic fungi use spores, such as conidia and zoospores, for infection, which may attach to the nematode cuticle or be ingested (Braga and de Araújo, 2014). Studies have shown that endoparasitic fungi can reduce the number of root-knot nematodes that create galls on tomatoes and alfalfa in greenhouse experiments (Liu *et al*., 2009).

These fungi exhibit varying degrees of diversity, particularly in their production of conidia per infected nematode. *Drechmeria coniospora* fungi produce a significant number of conidia, up to 10,000 per hyphal material, while *Hirsutella rhossoliensis* yields 100–1000 conidia per infected nematode. Conidia germinate immediately, and assimilative hyphae infiltrate and absorb the entire contents of the nematode body, enabling the fungus to penetrate the host’s outer layer (Nordbring-Hertz *et al*., 2006). *Drechmeria coniospora* is an aggressive endoparasitic fungus targeting nematodes. The *Drechmeria coniospora* YMF1.01759 strain exhibited excellent nematode-infecting ability by hindering nematodes from hatching their eggs, infecting them with spores, and producing active metabolites that killed them (Wan *et al*., 2021).

### *Egg- and Female-Parasitic Fungi*

Egg- and female-parasitic fungi are those that infect plant-parasitic nematode eggs and sedentary females using appressoria or zoospores (Lopez-Llorca *et al*., 2008). Key genera in this group include *Pochonia, Paecilomyces, Lecanicillium,* and *Nematophthora*. These fungi are of particular interest for the biological control of economically significant nematodes due to their ability to target sedentary life stages, such as eggs and developing juveniles, which are easier to infect because they are sessile. Additionally, these fungi can survive as saprobes in the rhizosphere, making them relatively easy to mass-culture. Among nematophagous fungi, only a few are considered promising biocontrol agents, with *Pochonia chlamydosporia* and *Paecilomyces lilacinus* being the most frequently isolated and studied (Siddiqui and Mahmood, 1996).

**Table 1**: Fungal species that parasitize the egg and female.

| **Species** | **Classification** | **Infection mode** |
|---|---|---|
| *Dactylella ovaparasitica* | Orbiliomycetes | appressoria |
| *Helicocephalum oligosporum* | Zygomycetes | Adhesive hyphae |
| *Lecanicillium psalliotae* | Deuteromycetes | appressoria |
| *Nematophthora gynophila* | Oomycetes | Zoospores |
| *Olpidium vermicola* | Chytridiomycetes | Zoospores |
| *Paecilomyces lilacinus* | Deuteromycetes | appressoria |
| *Pochonia chlamydosporia* | Deuteromycetes | appressoria |
| *Rhophalomyces elegans* | Zygomycetes | appressoria |

Egg- and female-parasitic fungi, which produce a higher amount of extracellular enzymes, are particularly effective at infecting nematode eggs (Yang *et al*., 2007). The efficiency of egg degradation varies among fungi, and the infection process can be influenced by the nematode host (Segers *et al*., 1999). The infection process of nematodes and their eggs by different nematophagous fungi generally follows a similar pattern (López-Llorca *et al*., 2008). *Pochonia chlamydosporia* targets the females and eggs of cyst and root-knot nematodes, developing branched mycelial networks that form appressoria on the eggshell (Viaene *et al*., 2006). *Paecilomyces lilacinus* is an opportunistic pathogen capable of infecting both nematodes and insects. It has been extensively studied and successfully used for controlling plant-parasitic nematodes (Kalele *et al*., 2007). This fungus infects eggs and cyst nematodes through the action of secreted hydrolyzing enzymes (Khan *et al*., 2004).

## Biocontrol Using Nematophagous Fungi

Biocontrol is regarded as an eco-friendly and sustainable alternative to pesticides (Rodrigues *et al*., 2023). This approach involves using microbial species, especially fungi, which have demonstrated significant antagonistic effects against plant-parasitic nematodes (PPNs) (Thambugala *et al*., 2020). While many fungi can be detrimental to nematodes, not all are reliable biocontrol agents; mere aggressiveness is not sufficient (Moosavi and Zare, 2020).

The two primary methods for utilizing nematode-killing fungi in biocontrol are: (1) introducing fungi directly into the soil; and (2) enhancing the activity of naturally occurring fungi through various modifications. Early research focused on fungi such as *Arthrobotrys* and *Monacrosporium* species, which trap nematodes. Later, endoparasitic fungi like *Hirsutella rhossoliensis* and *Drechmeria coniospora*, along with egg-parasitic fungi such as *Pochonia chlamydosporia*, were also employed as biocontrol agents (Liang *et al*., 2020).

## Nematophagous Fungi Used To Control Animal Nematodes

Nematophagous fungi show promise as biocontrol agents for managing animal nematodes, with several fungi successfully used to control parasitic nematodes in animals such as cattle, horses, sheep, and pigs. One notable example is the net-trapping predatory fungus *Duddingtonia flagrans*, which is widely used for this purpose. This fungus produces thick-walled resting spores, or chlamydospores, that can survive passage through the gastrointestinal tract of these animals (Soder and Holden, 2005).

*Duddingtonia flagrans* forms sticky traps that capture the developing larval stages of parasitic nematodes in the fecal environment. When chlamydospores of this fungus are administered daily to grazing animals over some time, they help reduce pasture infectivity and worm burden, particularly benefiting young lambs (Larsen, 2006). Studies conducted in France, Australia, the USA, and Mexico have demonstrated the strong biological control potential of *Duddingtonia flagrans* (Soder and Holden, 2005; Larsen, 2006).

*Pochonia chlamydosporia* is also an effective biocontrol fungus for managing animal nematodes (Braga *et al*., 2010; Ferreira *et al*., 2011). An evaluation of the in vitro ovicidal effects of four nematophagous fungi Pochonia chlamydosporia (isolates VC1 and VC4), *Duddingtonia flagrans* (AC001), and *Monacrosporium thaumasium* (NF34) on egg capsules of *Dipylidium caninum*, a cestode parasite of dogs, cats, and humans, showed that *Pochonia chlamydosporia* was effective against both the capsules and eggs of *Dipylidium caninum*. This indicates that *Pochonia chlamydosporia* holds potential as a biocontrol agent for this helminth (Araujo *et al*., 2009).

## Conclusion and Recommendations

Nematophagous fungi are a diverse and effective group of microorganisms that offer promising solutions for controlling nematode populations in both agricultural and veterinary contexts. Their classification into nematode-trapping, endoparasitic, and egg- and female-parasitic fungi underscores their specialized strategies for capturing and attacking nematodes. The ability of these fungi to thrive in nitrogen-poor soils and utilize various trapping mechanisms makes them valuable in biological control efforts. Among the different types, nematode-trapping fungi, such as those producing constricting rings and adhesive traps, are notable for their efficiency in capturing and digesting nematodes. Endoparasitic fungi, such as *Drechmeria coniospora*, effectively reduce nematode populations by internalizing and consuming nematode tissues. Egg- and female-parasitic fungi, like *Pochonia chlamydosporia*, offer significant potential for managing nematode eggs and sedentary life stages, contributing to effective control measures in agricultural settings. Biocontrol strategies using nematophagous fungi have demonstrated substantial efficacy in reducing nematode burdens in both plant and animal hosts. *Duddingtonia flagrans* and *Pochonia chlamydosporia* are particularly notable for their effectiveness in controlling parasitic nematodes in livestock and as biocontrol agents for helminth parasites.

Based on the above conclusion, the following recommendations were forwarded:

a. Continued research is needed to explore the full potential of various nematophagous fungi, particularly focusing on their efficacy, host specificity, and ecological impacts.

b. Nematophagous fungi should be integrated with other nematode management practices, such as crop rotation, soil health management, and chemical control, where necessary.
c. Efforts should be made to scale up the production of nematophagous fungi for commercial use for agricultural and veterinary applications.

## Contribution by Authors

All the authors contributed equally to writing the manuscript. The final manuscript was read by all authors and consented to publication.

## Conflict of Interests

There is no conflict of interest.

## Publisher Disclaimer

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