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Review Article

Nematophagous fungi: Far beyond the endoparasite, predator and ovicidal groups

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ABSTRACT

Knowledge of nematophagous fungi has increased dramatically over recent years, particularly with the advancement of molecular biology and omics sciences. However, most of this knowledge is restricted to the three traditional groups of nematophagous fungi: predatorial, opportunistic or ovicidal and endoparasitic. The present study supported the proposed classification of nematophagous fungi into five groups: nematode-trapping/predators, opportunistic or ovicidal, endoparasites, toxin-producing fungi and producers of special attack devices. This study also highlighted the analogy between special attack devices and real medieval weapons. Much study remains to be done to better understand some fungi and to discover new fungi with nematophagous and biological control potential.

Introduction

Nematophagous fungi are cosmopolitan microorganisms able to modify their saprophytic behavior to carnivorous, allowing them to feed on nematodes under unfavorable nutritional conditions. They are natural enemies of nematodes and have developed highly sophisticated strategies of infection (Braga and Araújo, 2014; Degenkolb and Vilcinskas, 2016).

There are over 700 nematophagous fungal species, from several phyla, such as the *Ascomycota*, *Basidiomycota*, *Chytridiomycota* and *Zygomycota*. Moreover, even organisms belonging to the phylum *Oomycota* have had their nematophagous activity described (Li et al., 2015).

Traditionally, those fungi are classified into three groups according to their characteristics of predation on nematodes: (1) nematode-trapping/predatorial, (2) opportunistic or ovicidal and (3) endoparasitic. This study briefly highlights the characteristics of each group. Predators produce modified hyphae called traps, with which using a mechanical/enzymatic process they bind and digest nematode larvae. There are a number of different traps already described in detail in the literature, for example: non-differentiated adhesive hyphae, three-dimensional adhesive networks, adhesive nodules, and constricting and non-constricting rings. The ovicidal group also uses traps in the process of predation. However, the target groups are eggs, cysts and nematode females. Endoparasites do not use hyphae for predation. These fungi are obligate parasites of nematodes, and use spores (conidia, zoospores) as infection structures, which may adhere to the nematode cuticle or be ingested (Braga and Araújo, 2014).

Recently, two new groups of nematophagous fungi have been proposed: toxin-producing fungi and producers of special attack devices (structures which mechanically damage the cuticle of nematodes) (Liu et al., 2009). These two and other fungi groups were the study subject of the current work.

Toxin-producing fungi

The study of nematophagous fungi was first described by Fresenius (1852) and Zopf (1888a,b). Drechsler (1937) described in greater detail the predatory activity of various species of these fungi. Over the years, several studies on the predatory behavior of nematophagous fungi have been recorded (Cooke, 1963; Cooke and Pramer, 1968; Monoson, 1968; Belder and Jansen, 1994; Araújo et al., 1995; Gives et al., 1999; Braga et al., 2009). However, even to the present time, most studies use nematode-trapping and endoparasitic groupings.

Since 1941 (Drechsler, 1941), it has been known that basidiomycetous fungi have the ability to feed on nematodes. These fungi are known as wood-root fungi, since their habitat is decaying wood. In this environment, the available nitrogen concentration is low. Thus, the capacity of fungi to feed on nematodes is a significant advantage, analogous to carnivorous higher plants that complement

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photosynthetic energy with protein from captured insects (Thorn and Barron, 1984; Barron and Thorn, 1987).

In relation to predatory activity, those fungi (commonly called mushrooms) have several features in their attack mechanisms on nematodes. *Nematoctonus* ("nematode killer") fungi act by means of mycelial adhesive traps or hourglass shape adhesive spores surrounded by a thick mucous sheath. The latter apparatus acts in the capture of nematodes by means of adherent contact, cuticle penetration and destruction of the nematode (Luo et al., 2006; Koziak et al., 2007a; Li et al., 2015). This genus presents a unique characteristic within the nematophagous fungi: depending on the species it may exhibit predatory, endoparasitic or even both behaviors. For example, *N. robustus* displays predatory action by traps, whereas *N. pachysporus*, *N. concurrens* and *N. haptocladus* have endoparasitic activity (Thorn and Barron, 1986; Askary and Martinelli, 2015; Li et al., 2015). *Nematoctonus* spp. endoparasitic action can be classified as parasitoid (predators who delegate the death of the prey to their descendants). It is also worth noting that these fungi have their teleomorph (sexual stage) in the genus *Hohenbuehelia (*Kumar and Kaviyarasan, 2012). Koziak et al. (2007b) described the geographical distribution of fungi from the genera *Nematoctonus* and *Hohenbuehelia*, especially in Costa Rica and showed that most of the works related to these microorganisms were in the northern hemisphere with a temperate climate.

Thorn et al. (2000) and Koziak et al. (2007a) in phylogenetic studies have provided evidence that *Hohenbuehelia* and *Pleurotus* genera belong to the family *Pleurotaceae*, from the *Agaricale* order, with nematophagous activity as the defining feature for this classification. The nematophagy apparently arose in the *Pleurotaceae* by means of the use of nematotoxic microdroplets produced by hyphae. However, this characteristic was maintained in the genus *Pleurotus*, while most species of *Hohenbuehelia* have lost it and have developed adhesive knobs on the hyphae or adhesive hourglass-shaped spores. Therefore, certain species of *Hohenbuehelia* which maintain both characteristics may be considered an evolutionary or adaptive link. Probably, from these "intermediate predators", the greatest loss of adhesive buttons in hyphae led to the development of the parasitoid activity (Koziak et al., 2007b).

The *Pleurotus* genus encompasses edible mushrooms that are commercially cultivated worldwide (Rosado et al., 2003). Like the other basidiomycetes, it forms fruiting bodies and its wild growth is as a saprophyte on decaying wood. The most common species of this genus is *P. ostreatus*, called the oyster mushroom. This genus produces powerful toxins that immobilize and lead to shrinkage of the head of nematodes prior to infection and digestion. Several species of *Pleurotus* have been shown to produce toxins with nematotoxic activity (Kwok et al., 1992; Nordbring et al., 1995; Satou et al., 2008).

Pleurotus ostreatus produces *trans*-2-decenoic acid, a toxin with nematotoxic action derived from linoleic acid. This toxin affects not only nematodes, but also insects and other fungi, possibly altering the permeability of cell membranes in their targets (Kwok et al., 1992). *Pleurotus pulmonarius* produces the following toxins: S-coriolic acid, linoleic acid, panisaldehyde, *p*-anisyl alcohol, 1-(4-methoxyphenyl)-1,2-propanediol and 2-hydroxy-(4′-methoxy)-propiophenone (Stadler et al., 1994a). Those and the above-cited toxins are shown in Table 1.

Pleurotus cystidiosus subsp. *abalonus* (subgen. *coremiopleurotus*) produces toxocysts surrounded by a paralyzing toxin of nematodes (Thorn and Tsuneda, 1993). *Pleurotus djamor, P. cornucopiae*, *P. levis*, *P. populinus, P. tuberregium* and *P. subareolatus* also have had their toxin production described (Thorn and Barron, 1984; Thorn and Tsuneda, 1993; Vilgalys et al., 1993; Hibbett and Thorn, 1994; Lopez-Llorca et al., 2006). Furthermore, the culture filtrate produced by *P. ostreatus, P. sajor-caju, P. florida, P. flabellatus* and *P. eryngii* demonstrated nematotoxic action (Shariat et al., 1994; Palizi et al., 2009). Khan et al. (2014) found that the crude extract from fruiting bodies of *Pleurotus ostreatus, P. florida* and *P. citronopileatus* had nematicidal activity on plant parasitic nematodes from the genera *Pratylenchus, Xiphinema, Tylenchorhynchus, Tylenchus, Helicotylenchus, Ditylenchus, Psilenchus, Aphelenchus, Hoplolaimus, Longidorus, Aphelenchoides* and *Paralongidorus*, and the extract from *P. citrinopileatus* showed the highest nematicidal activity.

Some fungi from the *Agaricales* order, *(Megacollybia platyphylla*, *Cyathus striatus* and *Kuehneromyces mutabilis*) and from the *Polyporales* order (*Daedalea quercina*, *Fomitopsis pinicola* and *Gymnopilus junonius*) also demonstrate effectiveness in destroying and colonizing nematodes by means of paralyzing toxins (Balaeş and Tănase, 2016).

Another reason proposed for the production of toxins capable of immobilizing invertebrates is a defensive role, preventing the consumption of the fungal colony by fungivorous invertebrates, such as some nematodes. It is known that some non-nematophagous fungi produce toxins with this function, but they merely paralyze their targets and do not consume them. However, the white rot fungus *Climacodon septentrionalis*, produces toxins that paralyze fungiphagous nematodes of the genus *Aphelenchoides* and destroy them later. Interestingly, this is the first example of such a substance in fungi that do not belong to the genus *Agaricus*. This polypore fungus produces toxin droplets much larger (20–45 μm) than those produced by *Pleurotus* spp. (1.5–3.0 μm) (Tanney and Hutchison, 2012).

It is worth pointing out that there are numerous other species of fungi producing toxins which act on nematodes. Li et al. (2007) reviewed in detail 179 different compounds from several chemical groups with nematicidal action, which were isolated mainly from deuteromycetes, ascomycetes and basidiomycetes. However few fungi fit into the nematophagous toxin-producing fungi group, since such fungi must have a way for the toxin to be applied and for the microorganism to feed on the nematode. Consequently, just a few fungi have this carnivorous character. A clear example is *Conocybe lactea*, which produces a toxin that in addition to paralyzing, can lead the death of the nematode, but at the end of the process the nematode is not consumed (Hutchison et al., 1996).

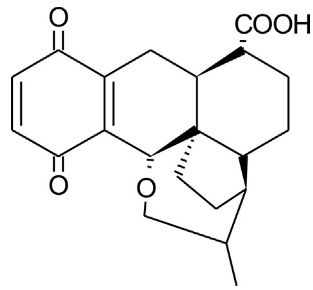
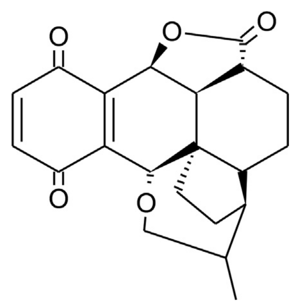
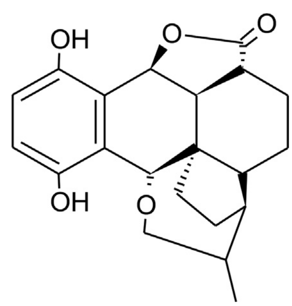
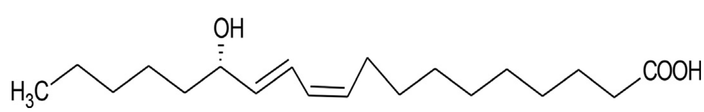
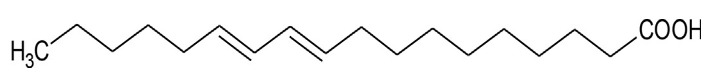
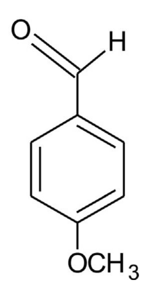
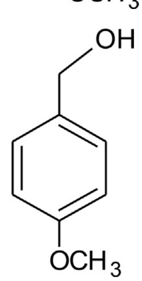
Myrothecium verrucaria strain X-16 is an atypical case of nematophagous fungus. This fungus can prey on eggs, second stage juveniles and adult nematodes of *Meloidogyne hapla*. It has not yet been defined how this fungus does this, but it is speculated that it produces proteases, chitinases and toxins (Dong et al., 2015).

Fungi producers of special nematode-attacking devices

Special attacking devices are similar to a sharp sword, causing damage to the nematode cuticle, resulting in extravasation of the inner content of the nematodes and allowing complete colonization of the nematode body by fungal hyphae. In general, the mechanism of action of these special devices can be explained as: 1) hyphae grow towards the cuticle of the nematode, and press on it; 2) a penetration peg is formed and penetrates the nematode cuticle; 3) hyphae colonize the interior of the nematode; and 4) hyphae project themselves from the infected nematode (Luo et al., 2004, 2006, 2007). Similar secreting appendages were found in *Conocybe lacteal*. However, this fungus after paralyzing and killing nematodes does not use them as food (Hutchison et al., 1996).

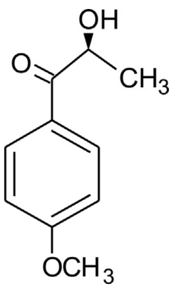
Coprinus comatus is a basidiomycetous fungus which produces an unusual structure designated a "spiny ball" that resembles a caltrop (Fig. 1). This structure is used as a special device by the fungus to damage the nematode cuticle and then, to consume them (Luo et al., 2004). This structure is tiny and by itself would not be able to inflect deadly damage on the nematode. However, many

Table 1
Some toxins produced by nematophagous fungi cited in the text.

Toxin	Chemical structure	Fungi	Reference
Dihydropleurotinic acid		*Nematoctonus robustus*	Stadler et al., (1994b)
Pleurotin		*Nematoctonus robustus*	Stadler et al., (1994b)
Leucopleurotin		*Nematoctonus robustus*	Stadler et al., (1994b)
S-coriolic acid		*Pleurotus pulmonarius*	Stadler et al.,(1994a)
Linoleic acid		*Pleurotus pulmonarius*	Stadler et al.,(1994a)
p-Anisaldehyde		*Pleurotus pulmonarius*	Stadler et al.,(1994a)
1-(4-Methoxyphenyl)-1,2-propanediol		*Pleurotus pulmonarius*	Stadler et al.,(1994a)

(*continued on next page*)

Table 1 (*continued*)

Toxin	Chemical structure	Fungi	Reference
2-Hydroxy-(4′-methoxy)-propiophenone		*Pleurotus pulmonarius*	Stadler et al.,(1994a)

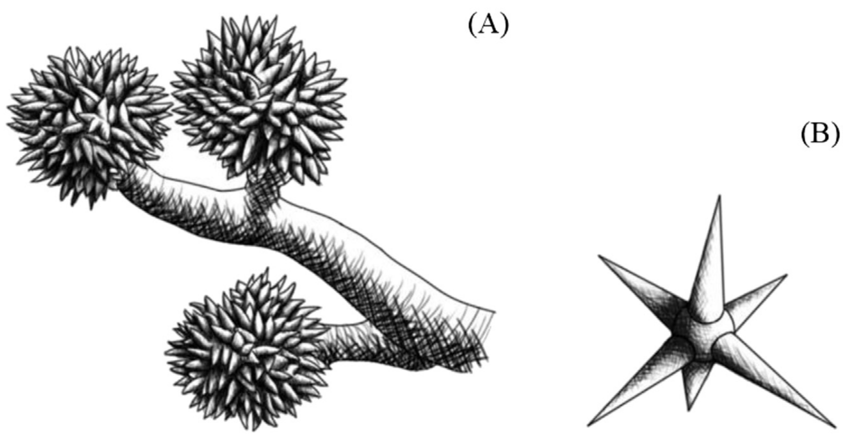


Fig. 1. (A) Special attack devices of basidiomycete nematophagous fungus *Coprinus comatus*, a designated unusual structure "spiny ball", which resembles the medieval weapon, the caltrop (B). This structure is used by the fungus to damage nematode cuticle together with toxins and thereafter to consume them.

spiny balls from *Cop. comatus* can cause lots of small cumulative cuts in the cuticle, which can lead to severe damage. However, this fungus also produces potent toxins to immobilize and kill nematodes. The efficiency of this special attack device is linked to the toxins produced. When the nematodes are injured by the projections of spiny balls, it is suggested that toxins may enter through the wound and act more efficiently and rapidly (Luo et al., 2007).

Stropharia species *(Strophariaceae*, *Basidiomycota)* are found in woods, grasslands, compost piles and animal manure. Its members are characterized by the formation of large cells with spikes called acanthocytes (Fig. 2) that can be compared to the medieval weapon of the ball and chain, where the fungus damages the cuticle of the nematode with the mechanical strength provided by its sharp projections (Luo et al., 2007). Farr (1980) did a detailed study of morphology and development of the acanthocytes, however, its function was still unknown. Luo et al. (2006) reported that these cells are special nematode-attacking devices from *S. rugosoannulata*. Subsequently, Zouhar et al. (2013) in the Czech Republic and Kong et al. (2013) in China, carried out others studies that confirm the action of acanthocytes against other nematodes.

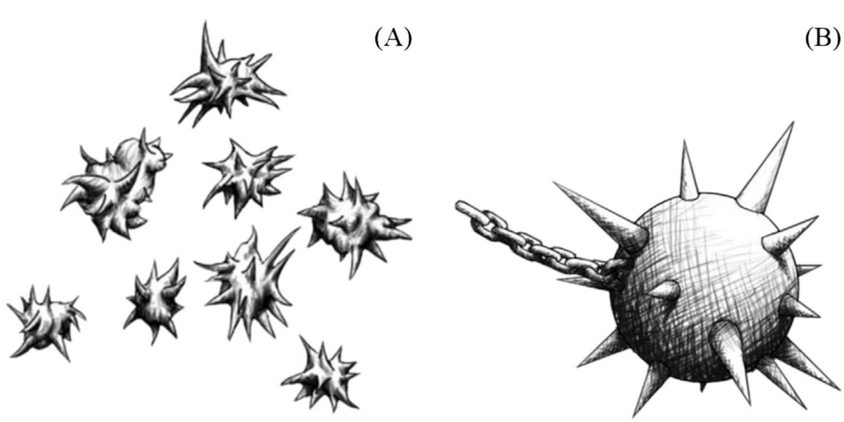


Fig. 2. (A) Special attack devices of nematophagous fungi from the genus *Stropharia* (Strophariaceae, Basidiomycota), large cells with spikes called acanthocytes, which resemble the medieval weapon, the ball and chain (B). The fungus damages the nematode cuticle with mechanical force provided by the sharp projections of acanthocytes, destroying and then, consuming the nematode.

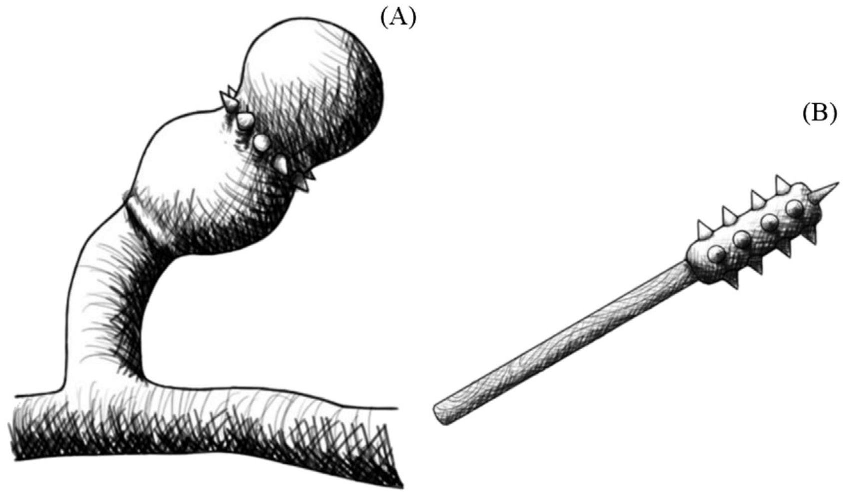


Fig. 3. (A) Special attack device of fungi from the genus *Hyphoderma* (Polyporales order), terminal globular cells, surrounded by a basal circle of spikes, called stephanocistos, which resemble the medieval weapon, the "morning star" (B). The stephanocyst adheres to the nematode cuticle and via a mechanical and enzymatic mechanism, a penetration peg is formed. Then, hyphae penetrate the cuticle and colonize the interior of the nematode.

In these three works mentioned above, the acanthocytes were tested against the following species of nematodes: *Panagrellus redivivus*, *Bursaphelenchus xylophilus*, *Meloidogyne incognita* and *Mel. hapla*.

Comparing the acanthocytes of *Stropharia* with the spiny balls of *Cop. comatus*, it can be observed that: acanthocytes (10 μm) are much larger than spiny balls (2 μm); the damage caused by acanthocytes on the nematode cuticle is much higher; spiny balls need toxin assistance to be successful in their nematicidal role.

Another special attack device described in the literature is produced by fungi from the genus *Hyphoderma*, order *Polyporales*. This genus produces stephanocysts—terminal globular cells, surrounded by a basal circle of spikes (Fig. 3). This device also resembles a medieval weapon, the morning star. Its mechanism of action is similar to that described above. The stephanocyst adheres to the nematode cuticle (usually on the tail or head) and via mechanical and enzymatic mechanisms, a penetration peg is formed. Then, hyphae penetrate the cuticle and colonize the nematode interior (Liou and Tzean, 1992; Tzean and Liou, 1993). Stephanocysts are also produced by *Crepidotus applanafus*, but in this case, the nematophagous activity has not been demonstrated (Senn-Irlet and Scheidegger, 1994).

A very peculiar attack device is used by endoparasitic fungi from the genus *Haptoglossa* (oomycetous fungi), namely the “gun cell” (Robb and Barron, 1982), resembling a Milenete Weapon or medieval cannon (Fig. 4). This device contains an elaborate inverted tubular system (Robb and Lee, 1986; Beakes and Glockling, 1998) that works as a syringe (Glockling and Beakes, 2000). The projectile head is laminated and compressible. When stimulated to fire, the projectile destroys the host cuticle and launches finger-like tubes directly at the target cytoplasm (Barron, 1987; Glockling and Beakes, 2000). Cell protoplasm then flows to the end of the tube that expands itself to form an oval sporidium, nucleated, inside the host (Glockling and Beakes, 2000). The device has structural variations from species to species, but the modus operandi is similar. The whole process is very fast, lasting less than 1 s (Glockling and Beakes, 2002). It should be emphasized here that this mechanism by itself, unlike others previously discussed, does not serve as a weapon to destroy the nematode cuticle for invasion and consumption by fungi, but rather serves as a complex input device for endoparasitic fungi of the genus *Haptoglossa* to enter their hosts.

Fungi with nematophagous activity

Filamentous fungi

In addition to the fungi mentioned above, a large variety of fungi also have nematophagous ability. However, they do not use the artifices classically described for nematophagous fungi (traps,

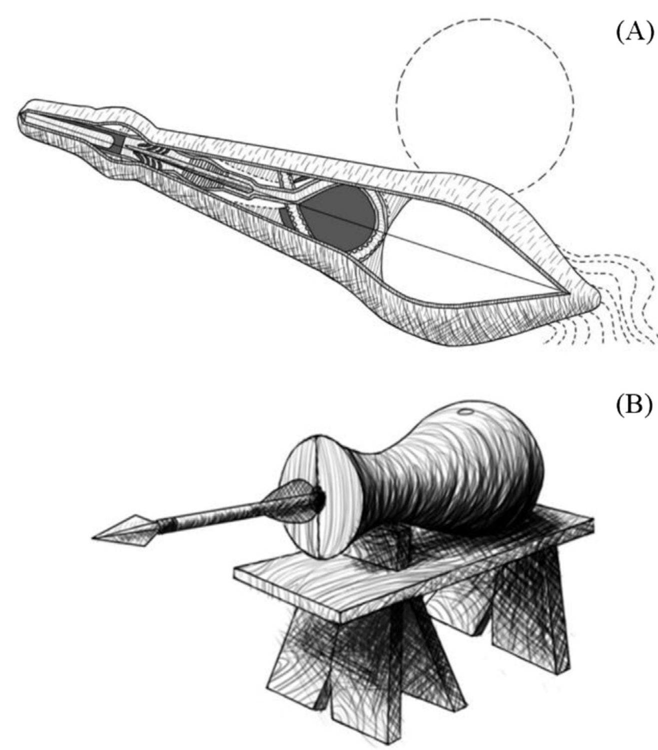


Fig. 4. (A) Special attack device of the endoparasitic fungi from the genus *Haptoglossa*, globular cells terminals. It is called a "gun cell", which resembles the medieval weapon the Milenete Weapon, a type of medieval cannon (B). This device contains an elaborate inverted tubular system. The projectile head is laminated and compressible. When stimulated to fire, the projectile destroys the host cuticle and launches finger-like tubes directly into the target cytoplasm. It should be emphasized here that this mechanism serves as an input device for endoparasitic fungi of the genus *Haptoglossa* into their hosts.

endoparasitism, toxins and special attack devices). Their attack methods are not very clear, but it is suggested that hydrolytic enzymes are critical in the process (Hallmann and Sikora, 1994). This section briefly discusses some cases.

Trichoderma species are endophytic, saprophytic and micopathogenic fungi that are widely used as biological control agents of plant parasitic nematodes *in vitro* and in greenhouses (Le et al., 2009; Affokpon et al., 2011; Zhang et al., 2014; Bogner et al., 2016; Dandurand and Knudsen, 2016). Successful parasitism by *Trichoderma* requires mechanisms to facilitate the penetration of the nematode cuticle or eggshell (Spiegel et al., 2004; Hallman et al., 2009; Szabó, 2014). Microscopic observation of *Trichoderma*-egg interactions showed evidence of all characteristic events of egg parasitism (coiling of hyphae around eggs, formation of appressorium-like structures, trophic hyphae growing inside the eggs) (Szabó, 2014). In this regard, at least two genes, chi 18-5 and chi 18-12, as components of the chitinolytic encoding system of *Tri. Harzianum*, seem to play a role in egg-parasitism (Szabó et al., 2012). Expression of chitinolytic enzymes by *T. harzianum* was also observed by Spiegel et al. (2004) in the presence of the nematode *Mel. javanica.* Activity of PRA1 trypsin-like protease and SprT serine protease of *Trichoderma* species against *Meloidogyne* juveniles was also observed (Suarez et al., 2004; Chen et al., 2009). Furthermore, comparative analysis of the protease expression profiles of *T. harzianum* revealed that 13 genes encoding peptidases are co-expressed in the *in vitro* nematode egg parasitism, suggesting these genes probably play a central role in the infection process (Szabó et al., 2013). In addition to direct antagonism, other mechanisms involved in the control of *Meloidogyne* by *Trichoderma* spp. are the production of metabolites and resistance induction (Yang et al., 2010, 2012). In addition, *Trichoderma* spp. have nematophagous action that has been described on *Mel. exigua*, *Mel. incognita*, *Mel. arenaria* and *Mel. javanica* eggs (Windham et al., 1989; Eapen et al., 2005; Sharon et al., 2007; Ferreira et al., 2008).

Endophytic and saprophytic fungi of the genus *Fusarium* also draw attention in relation to their application in the biological control of nematodes. Several non-pathogenic isolates of *Fus. oxysporum* reduced the rot of excised banana roots caused by *Pratylenchus goodeyi* (Speijer and Sikora, 1993). The main mechanism by which *Fusarium* spp. reduce nematodes parasitism is by means of penetration reduction of J2 juveniles (Hallmann and Sikora, 1994), besides systemic induction of resistance in the plant. However, parasitism is not a mechanism used by this genus to reduce plant parasites. On the other hand, some species such as *Fus. oxysporum*, *Fus. moniliforme*, *Fus. sulphureum* and *Fus. solani* complex have clearly demonstrated ovicidal action on *Toxocara canis* eggs, a zoonotic geohelminth (Ciarmela et al., 2010; Filho et al., 2013). It is also known that *Fusarium* spp. produce chitinases and probably these enzymes play an important role in the infection process of eggs (Mathivanan et al., 1998).

Although it is not the focus of this study, it is noteworthy that some endophytic fungi (such as *Acremonium* and *Syncephalastrum*) and arbuscular mycorrhizal (AM) have the ability to reduce nematode infestation with improvements in the growth of the infected plant, despite not always showing nematophagous action, but rather nematicidal activity (Li et al., 2015; Huang et al., 2016). Moreover, several other filamentous fungi genera have been described with nematophagous activity (*Penicillium, Aspergillus*) (Ruanpanun et al., 2010).

Entomopathogenic fungi

A common characteristic of all types of nematophagous fungi is that after contact with the cuticle of the nematode or eggshell, penetration occurs followed by content digestion, resulting in the formation of a new fungal biomass inside and later outside the nematode. Proteases and chitinases are key enzymes involved in this process (Soares et al., 2013, 2014; Braga et al., 2015).

Many different proteases and chitinases have been identified from nematophagous fungi (Yang et al., 2013). On the other hand, the pathogenic role of these hydrolytic enzymes was first described in entomopathogenic fungi, in particular *Beauvaria bassiana* and *Metarhizium anisopliae* (Bidochka and Khachatourians, 1987; St Leger et al., 1987). These fungi have had their entomopathogenic action widely described. However, some studies also showed that they have nematophagous activity, mainly due to enzyme action.

Metarhizium anisopliae has described activity on different plant parasitic juveniles, such as *Heterodera avenae* (Ghayedi and Abdollahi, 2013), *Rotylenchulus reniformis* (Sharma and Bhargava, 2008) and sugarcane nematodes (Zorilla, 2001). Moreover, *Met. brunneum* has ovicidal activity on *Ascaridia galli* eggs. Furthermore, it is suggested that *Met. brunneum* produces proteases which play an important role in egg infection (Cheta, 2015).

Beauvaria bassiana has very few reports on its nematophagous action. However, its enzymatic extract containing mainly proteases has proven activity against various plant parasitic nematodes of agricultural importance: *Mel. incognita*, *Mel. hapla*, *Aphelenchoides besseyi*, *Heterodera glycines* and *Caenarhabditis* sp. (Liu et al., 2008; Zhao et al., 2013).

Final considerations

Knowledge of nematophagous fungi has increased dramatically over recent years, particularly with the advancement of molecular biology and omics sciences. The genome and proteome of these fungi are becoming increasingly clear. However, most studies have been restricted to the three traditional groups of nematophagous fungi: predatorial, opportunistic or ovicidal and endoparasitic.

In a recent study, Locey and Lennon (2016) reported that there are about 1 trillion species of organisms on Earth. The magnitude of fungal diversity is estimated to be 1.5 million species, but only 5% of these have been described (Hawksworth, 2001). Thus, there is potential for the discovery of many fungi with nematophagous activity and which do not belong to traditional groups of nematophagous

Table 2
Nematophagous fungi classification into groups according to their predation characteristics on nematodes.

Group	Predation characteristics on nematodes
Nematode-trapping/ predatorial	Produce modified hyphae called traps, with which, by a mechanical/enzymatic process, they bind and digest nematode larvae.
Opportunistic or ovicidal	Produce modified hyphae called traps, with which, by a mechanical/enzymatic process, they bind and digest eggs, cysts and nematode females.
Endoparasitic	Use spores (conidia, zoospores) as infection structures, which may adhere to nematode cuticle or be ingested.
Toxin-producing	Secrete toxins that immobilize the nematodes, with posterior hyphae penetration through the cuticle and complete colonization of the nematode.
Producers of special attack devices	Produce special attacking devices that cause mechanical damage to the nematode cuticle, resulting in extravasation of the inner nematode contents and allowing complete nematode colonization.

fungi. A very small component of these microorganisms have been discussed in the present paper, but much study remains to be done to discover new fungi and to better understand the known fungi with nematophagous and biological control potential.

In conclusion, this study supports the classification of nematophagous fungi into five groups: nematode-trapping/predatorial, opportunistic or ovicidal, endoparasitic, toxin-producing and producers of special attack devices, as proposed by Liu et al. (2009) (Table 2).

Conflict of interest statement

The authors declare that have no conflict of interest.

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