

Hyperparasitic fungi—definitions, diversity, ecology, and research

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Abstract

Even parasites have parasites. By definition, a hyperparasite is an organism capable of parasitizing another parasite. Hyperparasitism caused by fungi is a common phenomenon in nature, but it has been poorly studied. This life history strategy evolved several times in the fungal tree of life, and is crucial in the maintenance of ecosystems as well as in the mediation of parasite–host interactions. Although the interest for hyperparasitic fungi is growing in the context of biological control, hyperparasitism is not ecologically and evolutionarily understood. This chapter summarizes the most relevant aspects of the terminology, diversity, and ecology of hyperparasitic fungi on both fungal and non-fungal hosts. We also discuss the problems related to molecular research on hyperparasitic fungi. As they represent a hidden source of diversity, it is necessary to increase sampling efforts and to undertake further morphological, molecular, and ecological studies to understand these fungi and their potential biotechnological and pharmaceutical uses.

1. Hyperparasitism

All living organisms can take part in parasitic relationships, either as parasites or as hosts (Combes, 2001; Krasnylenko *et al.*, 2021). Interactions between parasites and their hosts are typically regarded as closed one-to-one systems. In reality, however, these relationships involve complex multitrophic interactions (Kiss, 2001). The term “hyperparasite” refers to an organism that parasitizes another parasitic organism (**Fig. 1**). Hyperparasitism has been well documented for many groups of organisms, mainly insect parasitoids associated with parasitoid hosts, viruses that parasitize disease-causing protozoans, and parasitic flowering plants (Grybchuk *et al.*, 2018; Krasnylenko *et al.*, 2021; Sullivan, 1987). Hyperparasitism by fungi is poorly studied, even though it is thought to be rather widespread in nature (Haelewaters *et al.*, 2018a, 2021a; Parratt and Laine, 2016; Sun *et al.*, 2019). As fungi are able to parasitize organisms from different kingdoms (Moore *et al.*, 2020), this chapter focuses on fungal hyperparasites parasitic on both fungal and non-fungal hosts.

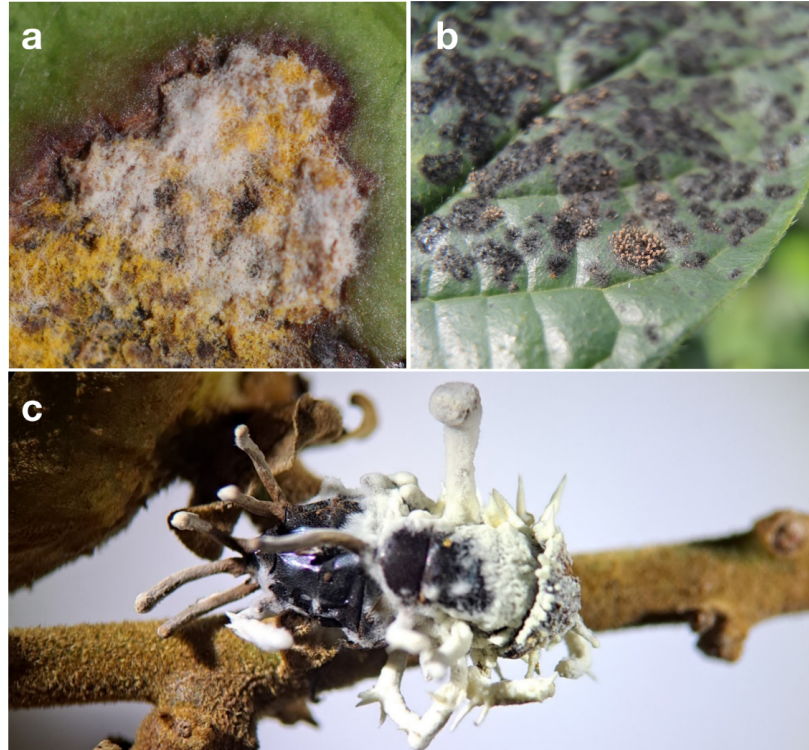


Figure 1: Examples of hyperparasitic fungi. a. The fungus *Akanthomyces lecanii* (white) growing on a lesion caused by the plant-pathogenic rust fungus *Hemileia vastatrix* (orange) on a leaf of *Coffea arabica*. b. *Atractilina parasitica* (orange) on colonies of *Meliola clerodendricola* (black mildew) on a leaf of *Clerodendrum capitatum*. c. *Niveomyces* sp. on *Ophiocordyceps dipterigena* on a dead fly, collected by Romina Gazis in Florida, USA (photo: Carlos Sendoya Corrales).

2. Relevant terminology

2.1. Hyperparasitism, mycoparasitism, and fungicolous fungi

The term hyperparasitism was introduced by Boosalis (1964) as an alternative for mycoparasitism and used in reference to the phenomenon of one fungus parasitic on another fungus. Although similar, these terms imply two different things. “Mycoparasitism” is a phenomenon in which one fungus (the mycoparasite) parasitizes another fungus (the host), regardless of whether the host is a saprotroph, mutualist, parasite, or commensalist (Karlsson *et al.*, 2018; Moore *et al.*, 2020). Moreover, mycoparasitism typically involves cell wall degradation and, in most cases, penetration of the host cells, e.g., as in the mycoparasitic activity of *Trichoderma harzianum* against *Rhizoctonia solani* (Altomare *et al.*, 1999; Atanasova *et al.*, 2013; Sun *et al.*, 2019).

In contrast, “hyperparasitism” occurs only if the host is also a parasite (Bermúdez-Cova *et al.*, 2022; Faticov *et al.*, 2022; Haelewaters *et al.*, 2018a; Piepenbring, 2015). It is important to note that hyperparasitic fungi use different methods to interact with their hosts (Boosalis, 1964; Jeffries, 1995), from hyphae or haustoria that penetrate host tissues to hyphal contact without penetration, to buffer cells that may facilitate flow of nutrients from host to parasite (Barnett and Lilly, 1958). For a fungus – or any other organism – to be considered a hyperparasite, it needs to negatively impact host fitness, otherwise it would be referred to

as a “hypermutualist” or “hypercommensal” (Kaishian *et al.*, 2023; Northrup *et al.*, 2021). A hyperparasitic interaction consists of *at least* three trophic levels (**Fig. 2**): a primary host, which is parasitized by a primary parasite, which serves as secondary host to a secondary parasite or hyperparasite.

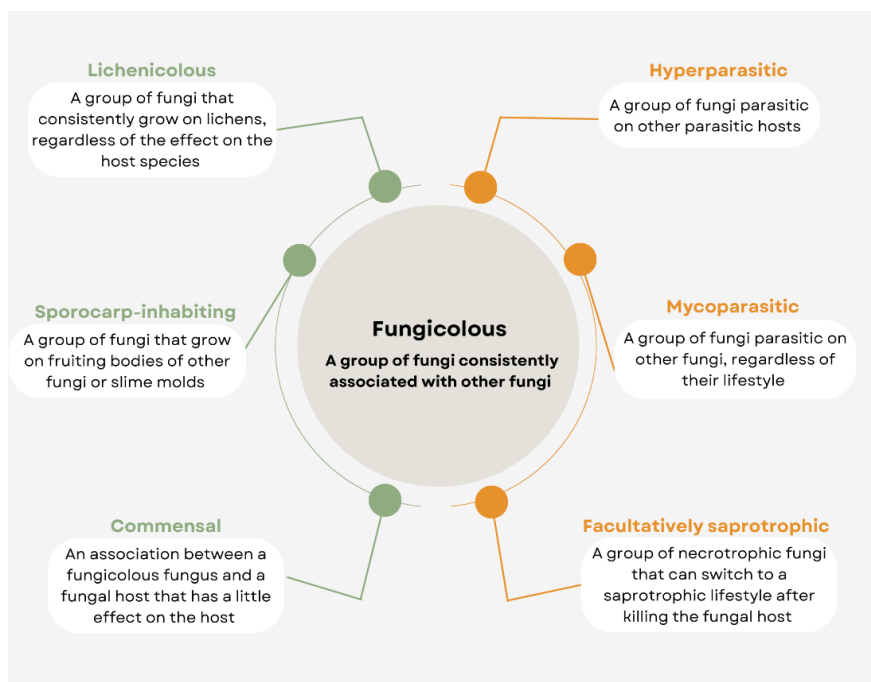


Figure 2: Definitions of important terms, based on Butler (1954), Hawksworth (1981), Jeffries and Young (1994), Alexopoulos (1996), Lawrey and Diederich (2003), Gams *et al.* (2004), Piepenbring (2015), Haelewaters *et al.* (2018a), Sun *et al.* (2019), Moore *et al.* (2020), Bermúdez-Cova *et al.* (2022), and Diederich *et al.* (2022). Definitions colored in green represent fungicolous fungi that cause little or have no effect on the fungal hosts, while definitions colored in orange represent fungi that have negative effects on the hosts.

The general term “fungicolous fungus” refers to a fungus that is consistently associated with other fungi (**Fig. 2**; Gams *et al.*, 2004; Hawksworth, 1981; Sun *et al.*, 2019). Researchers may also refer to fungi as fungicolous when the exact nature of the trophic relationship is not known (Barnett, 1963; Barnett and Binder, 1973). A distinction between hyperparasites, mycoparasites, and fungicolous fungi is made in the literature for several reasons. First, hyperparasitic fungi are frequently studied for their potential use in biocontrol of economically important parasites and pathogens (Brotman *et al.*, 2010). Second, they represent an opportunity to study trophic cascades and natural dynamics of predation in both host and parasite populations (**Fig. 3**; Parratt and Laine, 2016). Finally, parasitism of another organism that is strongly or obligately reliant on a specific host, has potential impacts on the dispersal and evolution of that organism, which parasites of non-pathogens may not experience.

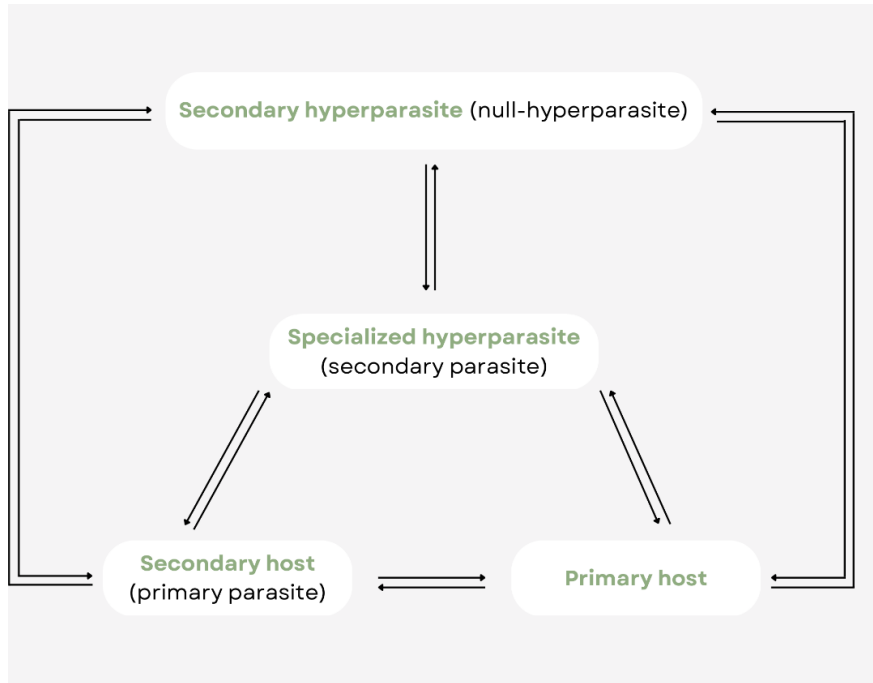


Figure 3: Multitrophic interactions between primary hosts, secondary hosts, and their specialized primary and secondary hyperparasites.

Some host species of hyperparasites do not necessarily have a fixed ecological strategy but rather exist on an ecological continuum during their life cycle, e.g., ranging from parasitism to saprotrophism. This can be illustrated by *Armillaria* spp., which are necrotrophs on various tree species. Once the host tree has died, *Armillaria* switches to a saprotrophic strategy, decaying the same tree substrate. *Armillaria* species themselves have been recorded as hosts for at least two agaricioid mycoparasites, namely *Collybia cookei* and *Entoloma abortivum* (see below). Nomenclatural issues may also arise when hyperparasites have multiple host species, some of which are parasites themselves whereas others may be saprotrophs. A prime example of this are species of *Trichoderma*, which infect both pathogenic and saprotrophic hosts (Jeffries and Young, 1994). In such cases use of the term “hyperparasite” maybe situational, depending on the ecological context of the host. Therefore, a “one-definition-fits-all” approach is unlikely to encapsulate the diversity of interactions observed in nature.

2.2. Null-hyperparasitism

It may happen that a hyperparasite is attacked by another parasite (Gállego Berenguer, 2007). Borkar (2020) refers to these secondary hyperparasites as null-hyperparasites, as they “nullify” the biocontrol activity of the primary hyperparasite. In a recent *in-vivo* experiment, this author showed that strains of *Aspergillus niger* and *Bacillus thermophilus* have the ability to parasitize the fungus *Trichoderma hamatum*, a common hyperparasite of the groundnut pathogen, *Sclerotium rolfsii*.

3. Types of hyperparasitic relationships

One of the ways fungal hyperparasites are defined is based on the state (living or dead) of the primary parasite (Barnett and Binder, 1973). Fungi that exploit living host tissue or cytoplasm are considered biotrophs,

whereas necrotrophs kill host cells and then utilize host biomass (Benjamin *et al.*, 2004; Jeffries and Young, 1994). Biotrophic hyperparasites typically have a narrower range of hosts and develop specialized structures to interact with their hosts (Jeffries, 1985, 1995). Examples of biotrophic hyperparasites and their parasitic hosts are given in **Table 1**. Many of these biotrophic hyperparasites form haustoria or specialized hyphal branches involved in absorption of food from host mycelia or sclerotia (Kirk *et al.*, 2008). Necrotrophs frequently use antifungal compounds in so-called hyphal interference (when the host is a fungus) or destroy the cell wall and membranes of host tissue to gain access to cellular contents, or use a combination of these strategies (Jeffries and Young, 1994).

Hyper-parasite	Primary parasite	Primary host	Evidence	Reference(s)
Agaricomycetes				
Collybia cookei	Armillaria spp.	Plant	Growth on host	Ludwig, 2012
Entoloma abortivum	Armillaria spp.	Plant	Carpophoroid morphology	Lindner <i>et al.</i> , 2001
Tremellomycetes				
Filobasidium elegans	Alternaria spp.	Plant	Growth on host	Bandoni <i>et al.</i> , 1991
Filobasidium flori-forme	Alternaria spp.	Plant	Haustoria observed in co-culture	Bandoni <i>et al.</i> , 1991
Filobasidium globisporum	Pleospora spp.	Plant	Growth on host	Bandoni <i>et al.</i> , 1991
Heteromyces tremellicola	Tremella philippinensis	Plant	Growth in host hymenium	Roberts and Spooner, 1998
Phragmoxenidium mycophilum	Rhizoctonia fusispora	Fungus	Haustoria observed - TEM	Oberwinkler <i>et al.</i> , 1990
Sigmogloea tremelloidea	Coniochaeta spp.	Plant	Haustoria observed - growth on host	Bandoni and Krug, 2000
Sirotrema parvula	Lophodermium pinastri	Plant	Haustoria observed - growth on host	Bandoni, 1986
Sirotrema pusilla	Hypoderma spp.	Plant	Haustoria observed - growth on host	Bandoni, 1986
Sirotrema translucens	Lophodermium spp., <i>Hypodermella</i> spp.	Plant	Haustoria observed - growth on host	Bandoni, 1986
Tetragonomycetes uliginosus	Rhizoctonia sp.	Plant	Haustoria observed - TEM	Oberwinkler and Bandoni, 1981
Tremella bryonec-triae	Bryonec-tria cuneifera	Plant	Growth on host	Döbbeler, 2019
Tremella colpo-maticola	Colpoma quercinum	Plant	Haustoria observed - direct interaction not observed	Hauerslev, 1999
Tremella karstenii	Colpoma juniperi	Plant	Haustoria observed - direct interaction not observed	Hauerslev, 1999

Mycoparasitic hyperparasites can also be classified based on the part of the host that is infected. For example, many species appear to attack only sclerotia (e.g., *Tyrannicordyceps fratricida*; Kepler *et al.*, 2012), spores (*Olpidium uredinis*; Berndt, 2013), or entire sporocarps (e.g., *Polycephalomyces* spp.; Kepler *et al.*, 2013).

Fungi categorized as hyperparasites include many mycoparasites, but as mentioned above, other fungi have non-fungal parasites as hosts. These include many animals such as insects and nematodes that are further discussed below. It is likely that there are important physiological and chemical differences among hyperparasites whose hosts belong to different kingdoms of life, and this is yet another way that hyperparasites can be categorized.

4. Diversity of hyperparasitic fungi

Hyperparasitic fungi are found across the fungal tree of life (**Fig. 4**), from Cryptomycota to former ‘zygomycetes’ to Basidiomycota (Gleason *et al.*, 2012; Jeffries, 1985; Lutz *et al.*, 2004) (**Fig. 5**). The genus *Trichoderma* (Sordariomycetes: Hypocreales) includes the best studied mycoparasites, some of which are hyperparasites of plant pathogens (Brotman *et al.*, 2010; Elad *et al.*, 1980). Hypocreales is an order with 320 genera that are rich in hyperparasites of fungi parasitic on plants, animals, and other fungi (Sung *et al.*, 2007; Wijayawardene *et al.*, 2022) (**Fig. 6**). *Akanthomyces lecanii* is a member of this order that exploits hosts in two different kingdoms: the coffee rust fungus, *Hemileia vastatrix* (Pucciniomycetes: Pucciniales), and the coffee scale insect, *Coccus viridis* (Vandermeer *et al.*, 2009). Having hosts that themselves are obligate associates with coffee plants as parasites, potentially enables this dynamic hyperparasite to maintain various reservoirs for dispersal through time and physical space in the environment (Jackson *et al.*, 2016). Many other prominent and well-studied groups of hyperparasites are representatives of Dothideomycetes. Some examples of hyperparasites in Dothideomycetes are *Ampelomyces* spp. (Pleosporales) on powdery mildews (Kiss *et al.*, 2004) and *Cladosporium* spp. (Capnodiales) on various parasitic hosts (Moricca *et al.*, 2005).

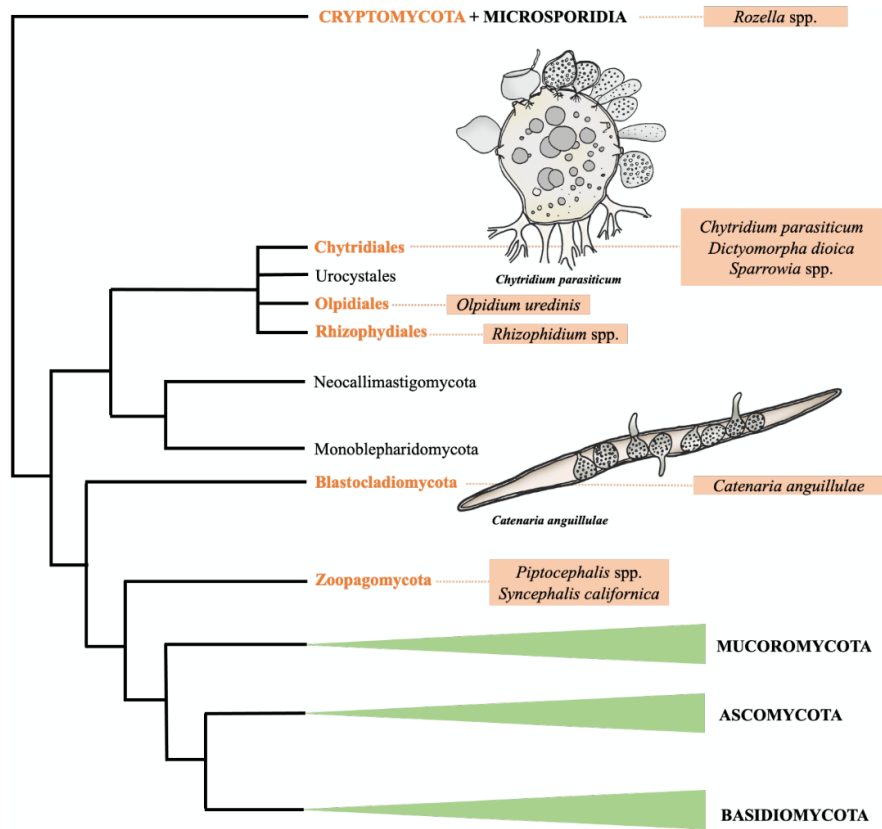


Figure 4: A simplified phylogeny of the Kingdom Fungi. Taxonomic groups in which hyperparasites are known are indicated in orange. Examples of hyperparasitic fungi are shown in orange boxes. Phylogenetic hypothesis taken and modified from Kendrick (2017), Spatafora et al. (2017), and Amses et al. (2022).

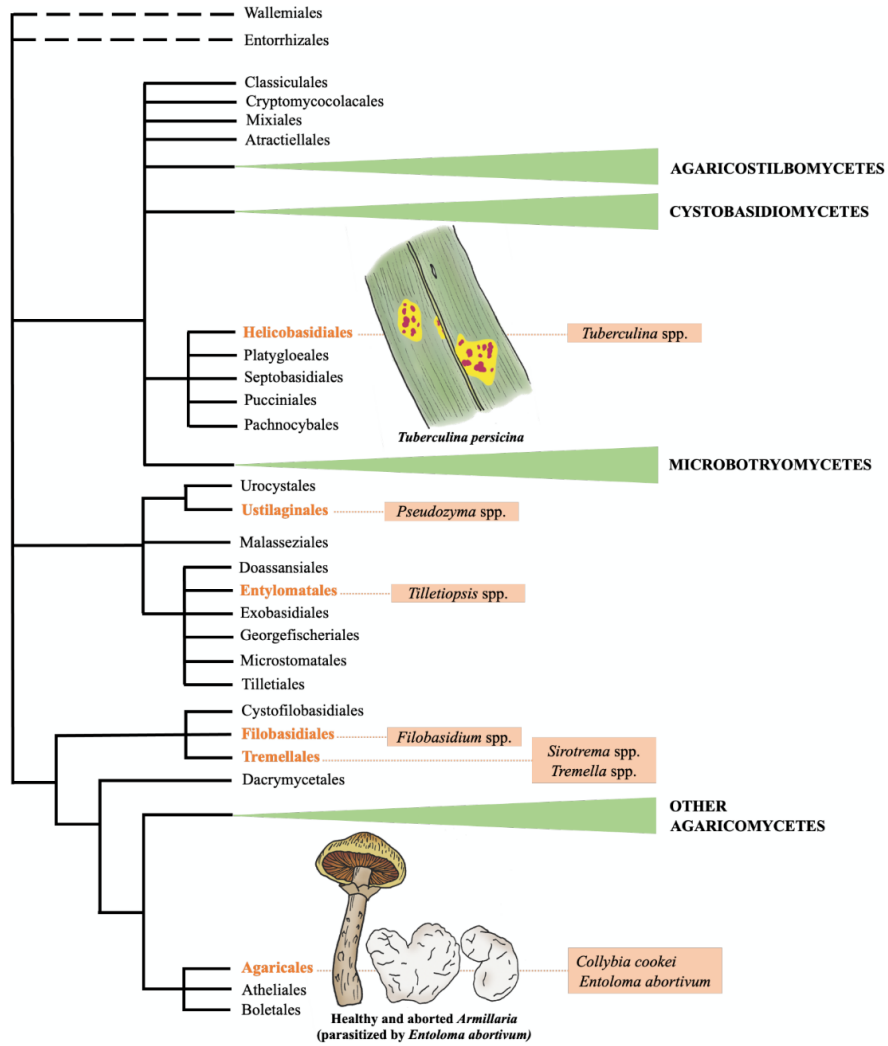


Figure 5: Simplified phylogenetic hypothesis of Basidiomycota. Taxonomic groups in which hyperparasites are known are indicated in orange. Examples of hyperparasitic fungi are shown in orange boxes.

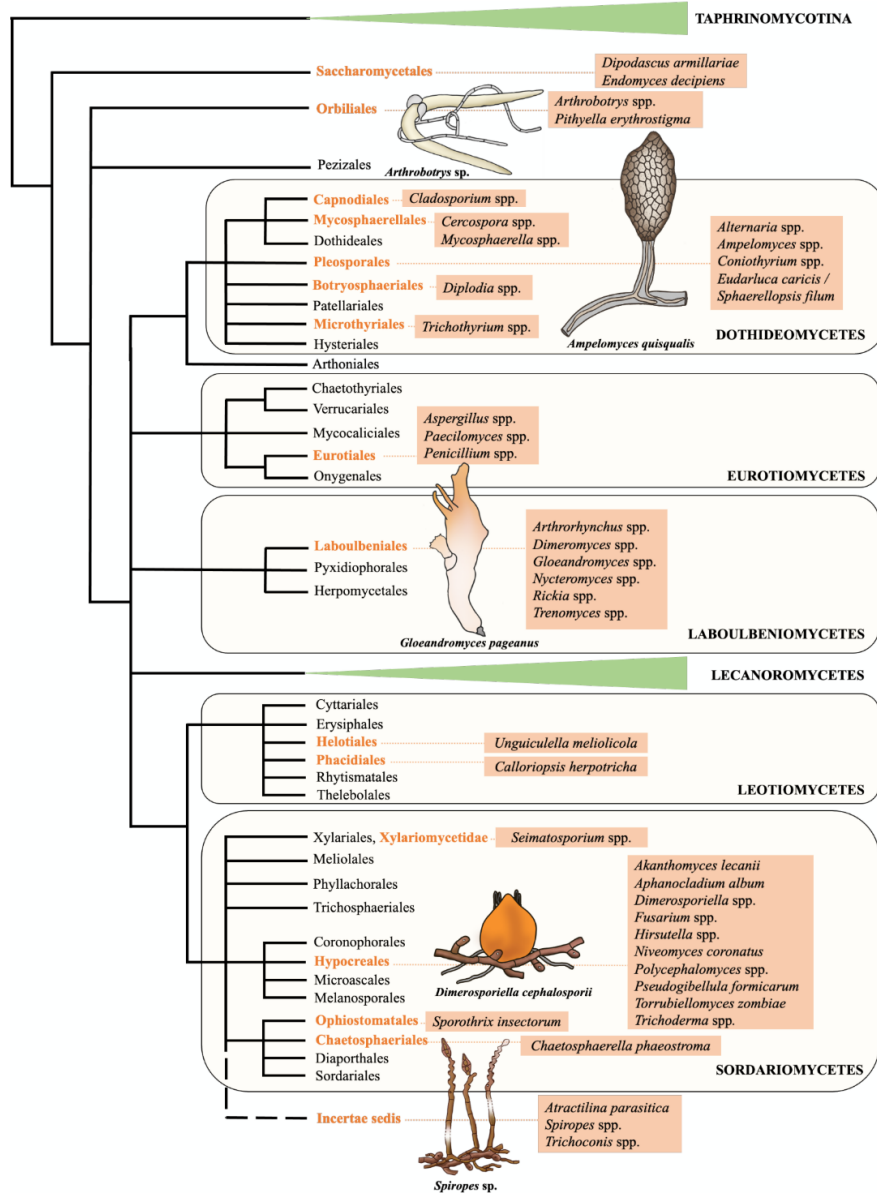


Figure 6: Simplified phylogenetic hypothesis of Ascomycota. Taxonomic groups in which hyperparasites are known are indicated in orange. Examples of hyperparasitic fungi are shown in orange boxes.

Fungal hyperparasites can also infect non-fungal hosts. The most common examples are nematophagous fungi able to parasitize plant-parasitic nematodes (Zhang *et al.*, 2020). Other than the egg stage, nematodes are capable of moving through their environments, posing a challenge to immobile and relatively slow-growing fungal parasites. However, some parasitic fungi have evolved to infect mobile stages of nematodes by means of specialized predation structures such as trapping structures to immobilize nematodes (Jiang *et al.*, 2017; Zhang *et al.*, 2020). Many lineages of fungi are known to trap or prey on parasitic nematodes, such as species of *Arthrotrichys*, *Monacrosporium* (Orbiliomycetes: Orbiliales), *Drechmeria*, *Fusarium*, *Harposporium*, *Hirsutella* (Sordariomycetes: Hypocreales), *Nematophthora* (Oomycota *incertae sedis*), *Paecilomyces* (Eurotiomycetes: Eurotiales), *Pochonia* (Sordariomycetes: Hypocreales), *Verticillium* (Sordariomycetes: Glomerellales), among others (Siddiqui and Mahmood, 1996).

4.1. Hyperparasites of plant-parasitic microfungi

Plant-parasitic microfungi are frequently colonized by hyperparasitic fungi that are able to penetrate the hyphae, the spores, and/or the reproductive structures of their fungal hosts (Gams *et al.*, 2004; Lumsden, 1992; Zhan *et al.*, 2014). Some of these parasites are specific to certain groups of plant pathogens and have garnered interest as biocontrol agents, such as *Ampelomyces quisqualis* (Dothideomycetes: Pleosporales) (**Fig. 7**), a naturally occurring hyperparasite of powdery mildews (Faticov *et al.*, 2022; Huth *et al.*, 2021). The most common plant-parasitic hosts include species of powdery mildews (Erysiphaceae), black mildews (Meliolales), tropical tarspot fungi (Phyllachorales), rusts (Pucciniales), and smuts (Ustilaginales and further orders) (Gams *et al.*, 2004; Hawksworth, 1981). Information about hyperparasitic fungi on plant-parasitic microfungi is scattered through literature, and there is no detailed treatment of biotrophic plant pathogens and their hyperparasites, as most publications deal with individual groups of fungi (Bermúdez-Cova *et al.*, 2022). Therefore, the following sections offer a summary of hyperparasites attacking these major groups of plant pathogens.

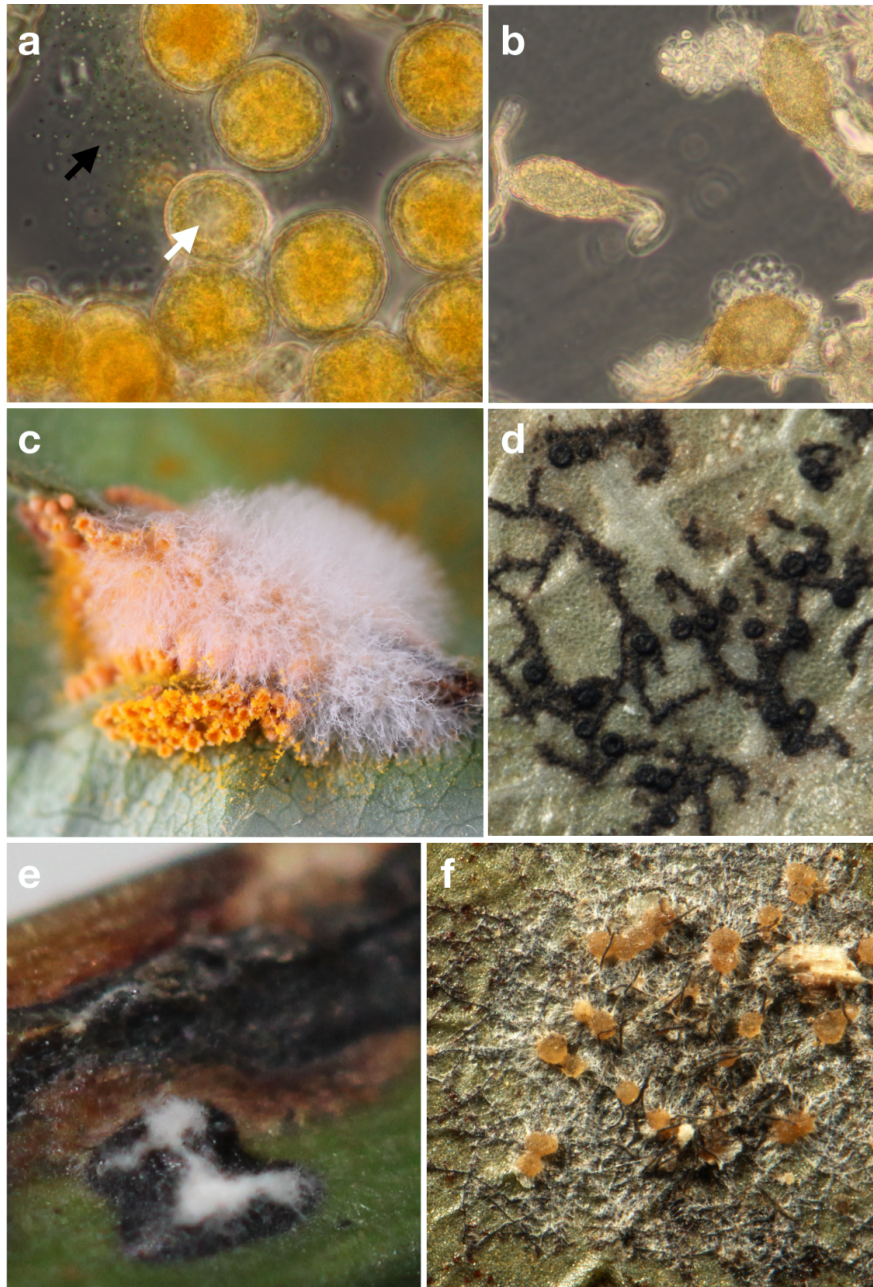


Figure 7: Hyperparasitic fungi on plant-associated microfungi. a. Zoospores (black arrow) and zoosporangium (white arrow) of *Olpidium uredinis* inside a urediniospore of a rust fungus (Pucciniales). b. Picnidia of *Ampelomyces quisqualis*. c. *Fusarium* sp. on aecidia of *Puccinia coronata* on a leaf of *Rhamnus cathartica*. d. *Trichothyrium* sp. on a colony of *Meliola* sp. e. White hyphomycete on pycnidia of *Camarotella costaricensis* (Sordariomycetes: Phyllachorales) on a leaf of *Acrocomia aculeata*. f. *Paranectriella* sp. on a colony of *Meliola* sp.

4.1.1. *Hyperparasites of powdery mildews*

Species of Erysiphaceae (Leotiomycetes: Helotiales; Haelewaters *et al.*, 2021b), the powdery mildews, are frequently attacked by species of hyperparasitic fungi belonging to the genus *Ampelomyces*, such as the type species *A. quisqualis* (Faticov *et al.*, 2022; Huth *et al.*, 2021; Parratt and Laine, 2016; Tillenaere *et al.*, 2014). This is a destructive, obligate, intracellular parasite that occurs on both the sexual and asexual stages of Erysiphaceae (Hawksworth, 1981). *Ampelomyces quisqualis* is able to form pycnidia inside the fungal host perithecia and/or hyphae, resulting on the reduction or complete halt of sexual and asexual sporulation of the powdery mildew species (Hawksworth, 1981; Legler *et al.*, 2016). Powdery mildew colonies infected by *Ampelomyces* spp. are easily identified by a change in color, from white to brown (Faticov *et al.*, 2022; Németh *et al.*, 2019). While molecular studies have revealed that *Ampelomyces* may comprise at least four to seven species, the taxonomy within the genus is unresolved (Németh *et al.*, 2019, 2021).

There are other less common species of fungi reported to be growing on colonies of Erysiphaceae, such as the hyphomycetes *Acremonium byssoides*, *Akanthomyces lecanii*, and *Aphanocladium album* (Sordariomycetes: Hypocreales) (Hawksworth, 1981). The usually saprotrophic fungus *Cladosporium oxysporum* (Dothideomycetes: Capnodiales) was found to arrest the development and maturation of the ascospores of *Phyllactinia corylea* (Rao and Pavgi, 1978). Species of *Pseudozyma* (Ustilaginomycetes: Ustilaginales) and *Tilletiopsis* (Exobasidiomycetes: Entylomatales) are occasionally found parasitizing powdery mildews (Gafni *et al.*, 2015; Gams *et al.*, 2004; Klecan *et al.*, 1990).

4.1.2. *Hyperparasites of black mildews*

An approximate 200 species of fungi are reported to be hyperparasitic on colonies of black mildews (Sordariomycetes: Meliolales). They include organisms from diverse systematic groups, and therefore comprise species producing a high diversity of reproductive structures, such as synnemata, pycnidia, apothecia, perithecia, and catathecia, among others (Bermúdez-Cova *et al.*, 2022). The most common hyperparasites of black mildews are species of the genera *Atractilina*, *Spiropes* (*Pezizomycotina incertae sedis*), *Dimerosporiella* (Sordariomycetes: Hypocreales), and *Trichothyrium* (Dothideomycetes: Microthyriales) (Bermúdez-Cova *et al.*, 2022; Deighton and Pirozynski, 1972; Ellis, 1968; Pirozynski, 1977; Rossman, 1987; Rossman *et al.*, 1999). Hyperparasites of Meliolales are contact-biotrophic fungi and prevent their host from producing spores and ascomata (Stevens, 1918; Toro, 1952). The current systematic position of almost all species of hyperparasitic fungi of Meliolales is unknown due to two reasons: the description of many of these predated the molecular era and technical problems make DNA extractions and PCR amplifications challenging (see **7. Molecular studies of hyperparasitic fungi**).

4.1.3. *Hyperparasites of tropical tar spot fungi*

Tropical tar spot fungi (Sordariomycetes: Phyllachorales), along with Erysiphaceae and Meliolales, are among the most frequently hyperparasitized fungal lineages (Cannon, 1991; Hawksworth, 1981). Parbery (1978) listed some common hyperparasitic fungi of *Phyllachora* and *Linochora* species, namely *Phaeodothis winteri* (Dothideomycetes: Pleosporales), as well as species of *Cercospora*, *Mycosphaerella* (Dothideomycetes: Mycosphaerellales), *Seimatosporium* (Sordariomycetes: Amphisphaeriales), and other dematiaceous fungi. Other potential hyperparasites of Phyllachorales are cited by Baker and Dale (1951), Sivanesan and Kranz (1975), and Sutton (1980). Caution is warranted when interpreting fungal associates of tar spot fungi. The anamorph–teleomorph connections in Phyllachorales are not well understood; asexual states may be misinterpreted as hyperparasites, and vice versa (M. Mardones, personal communication). Moreover, it may be difficult to determine whether an associated fungus is a hyperparasite of the tar spot fungus or simply uses the cavities or the lesions as entrance for direct plant parasitism (Hawksworth, 1981).

Hyperparasitic fungi of Phyllachorales use different strategies to infect their hosts. Some hyperparasites grow through the perithecial ostiole of the tar spot fungus to expose their conidiophores, whereas others form a narrow layer of conidiogenous cells closely adjacent to the inner perithecial layer of the phyllachorean fungus and remain almost invisible on the leaf surface (M. Mardones, personal communication). The coelomycete

Diplodia sp. (Dothideomycetes: Botryosphaeriales), for example, forms its pycnidia inside the ascomata of *Phyllachora sacchari* (Rao, 1967). Hyperparasitized colonies of *Phyllachora* can be recognized by their dull surface and the necrotized host tissue around them (Gams *et al.*, 2004).

4.1.4. *Hyperparasites of rusts*

More than 80 species and approximately 30 genera of fungi can parasitize rust fungi (Pucciniomycetes: Pucciniales) and are, mostly asexual forms of Ascomycota (Gams *et al.*, 2004; Hawksworth, 1981; Kranz, 1981; Leinhos and Buchenauer, 1992; Zhan *et al.*, 2014; Zheng *et al.*, 2017). In the genus *Cladosporium*, *C. aecidiicola*, *C. cladosporioides*, *C. pseudocladosporioides*, *C. sphaerospermum*, *C. tenuissimum*, and *C. uredinicola* have been reported as hyperparasites of rust fungi (Keener, 1954; Mendgen, 1981; Moricca *et al.*, 1999; Sharma and Heather, 1978; Srivastava *et al.*, 1985; Sun *et al.*, 2019; Torres *et al.*, 2017; Traquair *et al.*, 1984; Tsuneda and Hiratsuka, 1979; Vandermeer *et al.*, 2009; Wang *et al.*, 2016; Zhan *et al.*, 2014). *Cladosporium* species are in close contact with the cells of the rust fungus, through formation of appressoria and penetration of the host cells by mechanical force or through the production of lytic enzymes (Assante *et al.*, 2004; Moricca *et al.*, 2001; Nasini *et al.*, 2004).

Species of the genus *Tuberculina* (Pucciniomycetes: Helicobasidiales) are known only to be parasitic on rust fungi (in their asexual stage), living in association with more than 150 host species from at least 15 genera (Hawksworth, 1981; Lutz *et al.*, 2004). The most common species are *T. maxima* and *T. persicina*, reported from species of *Cronartium* and *Gymnosporangium*, respectively (Hawksworth, 1981; Hubert, 1935). *Tuberculina* species have an alternating life cycle (Lutz *et al.*, 2004) with morphologically and ecologically distinct sexual and asexual stages, which were formerly classified into different genera: *Helicobasidium* for the sexual stage and *Tuberculina* for the asexual stage.

In their asexual stage, *Tuberculina* species produce lilac to violet sporodochia-like structures growing on the sori of rust fungi. Cytoplasmic contacts between host and parasite are facilitated by micrometer–fusion pores, structures that are unique among Basidiomycota (Bauer *et al.*, 2004). In the sexual stage, these species are phytopathogens that form purplish crust-like sporocarps on living and dead plant material, causing violet root rot on a multitude of plant host species.

Quasiramularia phakopsoricola (Ustilaginomycetes, Basidiomycota) is a mycoparasite on the rust *Phakopsora ampelopsidis* and represents the only known mycoparasitic member among Ustilaginomycotina (Kolařík *et al.*, 2021). This hyperparasite resembles the hyphomycetous morphology of *Ramularia* species (Dothideomycetes, Ascomycota), and its affinity to Basidiomycota was only proven by phylogenetic analyses. Sexual reproduction in this species is not known, and the host-parasite interaction mechanism remains to be investigated.

The most common hyperparasite of rust fungi is the pycnidial fungus *Sphaerellopsis filum* (Dothideomycetes: Pleosporales). This is a biotrophic hyperparasite that grows mostly in the uredinia of its host (Gams *et al.*, 2004; Keener, 1934). Through the production of enzymes, it is able to penetrate urediniospores to inhibit their germination (Carling *et al.*, 1976; Leinhos and Buchenauer, 1992; Stähle and Kranz, 1984). *Sphaerellopsis filum* has a broad host range among rust fungi; and has been documented from over 360 species in 30 genera (Leinhos and Buchenauer, 1992).

Akanthomyces lecanii and *Aphanocladium album* (Sordariomycetes: Hypocreales) are necrotrophic hyperparasites that penetrate and destroy spores of *Puccinia graminis* (Gams *et al.*, 2004; Leinhos and Buchenauer, 1992). The infection of urediniospores by *A. lecanii* induces precocious teliospore formation, which may be a self-defense mechanism of the rust fungus against the hyperparasite (Koç and Défago, 1983). Species of *Acremonium*, *Fusarium*, *Simplicillium* (Sordariomycetes: Hypocreales), *Alternaria* (Dothideomycetes: Pleosporales), and *Verticillium* have also been reported as hyperparasites (Buchenauer and Leinhos, 1982; Gams, 1975; Wollenweber, 1934; Zheng *et al.*, 2017). Many other potential parasites of rust fungi are cited by Hawksworth (1981), Gowdu and Balasubramanian (1988), Leinhos and Buchenauer (1992), and Gams *et al.* (2004).

4.1.5. Hyperparasites of smuts and bunts

Reports of hyperparasitic fungi on smut and bunt fungi (Basidiomycota: Ustilaginomycotina) are scarce (Hawksworth, 1981). Species of *Fusarium* may grow on *Ustilago* spp., and the infections by these parasites can render the edible galls produced by *Ustilago maydis* poisonous (Gams *et al.*, 2004; Wollenweber and Reinking, 1935). *Aphanocladium album*, a common parasite of rust fungi, has also been reported growing on teliospores of Ustilaginales (Koç and Défago, 1983). Species of *Tilletiopsis* (Exobasidiomycetes: Entylomatales) have been found growing on lesions caused by *Entyloma* (Exobasidiomycetes: Entylomatales), although their hyperparasitic activity has not been demonstrated (Brady, 1960).

4.2. Zoosporic hyperparasites

Zoosporic hyperparasites have been reported among Fungi in Blastocladiomycota, Chytridiomycota, and Cryptomycota, and among zoosporic fungus-like protists such as Hyphochytriomycota, Labyrinthulomycota, and Oomycota (Gleason *et al.*, 2014), all three of which are now recognized as belonging to the Stramenopila lineage of Eukaryotes (Keeling and Burki, 2019; Wijayawardene *et al.*, 2022). Zoosporic parasites can grow as epibionts on the surface of their hosts by means of specialized structures such as rhizoids, or as endobionts (i.e., intracellularly) being completely submerged within their hosts (Held, 1973, 1974; Gleason *et al.*, 2012; Karling, 1960). There is a third type of association, such as in hyphal-forming zoosporic organisms, where interactions between hyphae of the hyperparasite and the primary parasite can be observed (Gleason *et al.*, 2014). This is the case, for example, for the interactions of the oomycete *Pythium oligandrum* and hyphae of its plant-parasitic oomycete hosts, *Pythium* spp. and *Phytophthora* spp. (Benhamou *et al.*, 1999).

Some parasites have evolved to grow on closely related host taxa. These parasites are known as “adelphoparasites” (Goff and Zuccarello, 1994). Species of *Pythium* are often parasitized by species of the same genus, such as *P. acanthium*, *P. mycoparasiticum*, *P. nunn*, *P. oligandrum*, and *P. periplocum* (Berry *et al.*, 1993; Deacon, 1976; Deacon and Henry, 1978; Lutchmeah and Cooke, 1984; Martin and Hancock, 1987; Vesely, 1977). It is also common among chytrids to be parasitized by other chytrids. Species of the same genus may be both parasite and host and, in some cases, individuals of the same species parasitize each other (Frenken *et al.*, 2017; Karling, 1960). For example, *Chytridium parasiticum* is a hyperparasite of *Chytridium suburceolatum*, which is itself a parasite on *Rhizidium richmondense* (Gleason *et al.*, 2014; Willoughby, 1956). Adelphoparasitism is a common phenomenon among zoosporic hyperparasites, but it is also known in other taxa, such as in *Tyrannicordyceps* and *Claviceps* species (Kepler *et al.*, 2012).

The most comprehensive taxonomic treatments on zoosporic hyperparasites were done by Karling (1942a, 1942b) and Sparrow (1960). More studies, however, are necessary to describe both the diversity of these organisms and their interactions.

4.3. Sordariomycetes hyperparasites of zombie-ant fungi

The genus *Ophiocordyceps* contains species of insect pathogens and mycoparasites (**Fig. 8**), a few of which are famous because of their ability to manipulate the behavior of their insect hosts (Eberhard *et al.*, 2014; Roy *et al.*, 2006). Species of the *Ophiocordyceps unilateralis* clade induce climbing and biting behaviors in ant hosts of the tribe Camponotini (Evans *et al.*, 2011). This is known as “summit disease”, which is common to many arthropod parasites across multiple lineages of the fungal kingdom (Evans, 1989; Marikovsky, 1962; Roy *et al.*, 2006). These behavioral manipulations increase transmission chances of *Ophiocordyceps* fungi and have earned them the moniker “zombie-ant fungi”. These pathogens are not immune to becoming parasitized themselves. While formal descriptions of hyperparasites of zombie-ant fungi are few and scattered, the presence of hyperparasites has certainly been noted by mycologists who study *Ophiocordyceps* across the globe (Andersen *et al.*, 2012; Araújo *et al.*, 2020, 2022; Mongkolsamrit *et al.*, 2021).

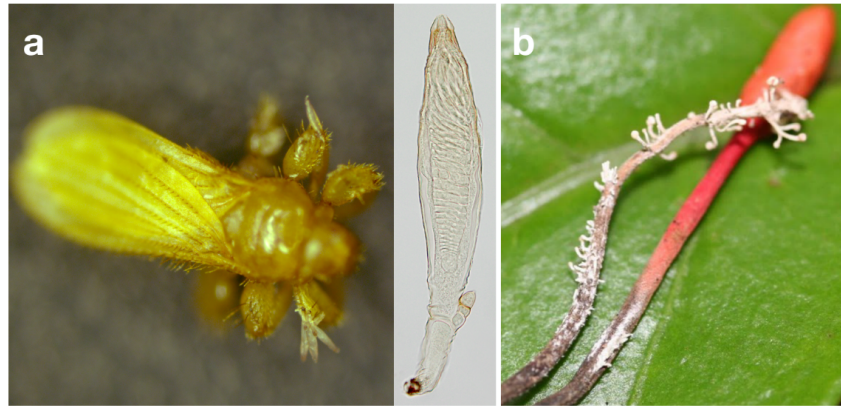


Figure 8: Hyperparasitic fungi on insect hosts. a. *Nycteromyces streblidinus* on the legs of a *Trichobius joblingi* bat fly (left) collected from a *Carollia perspicillata* bat, and a female thallus of the Laboulbeniales microfungus at higher magnification (right). b. *Polycephalomyces* cf. *yunnanensis* (Hypocreales: Ophiocordycipitaceae) parasitizing *Ophiocordyceps nutans* (Ophiocordycipitaceae), a pathogen of stink bugs (Hemiptera: Pentatomidae). In the background, a bright pink uninfected ascoma of *O. nutans* is shown for contrast.

Multiple hyperparasite species can be associated with a single *Ophiocordyceps*–ant species pair. Three species – *Pseudogibbellula formicarum*, *Torrubiella carnata/liberiana/pseudogibbellulae* (Hypocreales), and *Sporothrix insectorum* (Ophiostomatales) – were found on *Ophiocordyceps palthothyrei*, which infects *Palthothyreus tarsatus* ants in Ghana (Araújo *et al.*, 2020). Additionally, two recently described hyperparasite species, *Niveomyces coronatus* and *Torrubiellomyces zombiae*, are associated with *Ophiocordyceps camponoti-floridani*, infecting and manipulating the carpenter ant *Camponotus floridanus* in Florida, USA (Araújo *et al.*, 2022). This suggests that future work on the hyperparasites of zombie-ant fungi will likely reveal a wealth of undescribed species that could be mined for their abilities to affect animal-infecting fungi.

Beyond documenting their diversity, the extent to which hyperparasites affect the life span and transmission of their *Ophiocordyceps* hosts, as well as their molecular and cellular mechanisms remain to be investigated. A field study on *O. camponoti-floridani* suggests that both hyperparasites associated with this ant parasite co-occur in the same wilderness areas and harshly limit its transmission chances; when hyperparasitized, 10–40% of ant cadavers were observed with perithecia of *O. camponoti-floridani*, while this percentage was significantly higher (76%) in non-parasitized *Ophiocordyceps* (Will *et al.*, 2022). However, only 4% of *Ophiocordyceps*-manipulated ant cadavers had visible hyperparasite growth within the 1-year timespan of the study. Moreover, while new *T. zombiae* infections were found year-round, *N. coronatus* appeared to have a more seasonal occurrence (Will *et al.*, 2022). The disease dynamics of hyperparasites associated with *Ophiocordyceps* spp. might add a species-specific layer of complexity to the understanding of these multitrophic interactions.

4.4. Laboulbeniales hyperparasites

Laboulbeniales are an order of enigmatic microfungi that form three-dimensional multicellular thalli instead of hyphae and are associated with a living host for the entire duration of their life cycle (Haelewaters *et al.*, 2012). Hosts include a variety of Arthropods: harvestmen and mites (subphylum Chelicerata: class Arachnida); millipedes (Myriapoda: Diplopoda); and numerous insect lineages (Hexapoda: Insecta), such as ants, beetles, cockroaches and termites, crickets, earwigs, flies, lice, thrips, and true bugs. Some of the

arthropod hosts of Laboulbeniales are parasites themselves, which results in hyperparasitic associations. The study system that is researched most in depth is that of Laboulbeniales associated with bat flies (Diptera: Nycteribiidae and Streblidae), which are bloodsucking ectoparasites of bats (Mammalia: Chiroptera).

Bat fly-associated Laboulbeniales were discovered in the 1850s, although at that time known as acanthocephalan worms (Kolenati, 1857). By 1932, the year that marks the death of Roland Thaxter who described hundreds of species of Laboulbeniales, five species of Laboulbeniales from bat flies were described. Twenty years later, Merola (1952) described a sixth species, and it took another 65 years for any taxonomic contributions in this system (Haelewaters *et al.*, 2017b). To date, 18 species in four genera are known to parasitize bat flies (Haelewaters *et al.*, 2021a; Liu *et al.*, 2020; Van Caenegem *et al.*, 2023; W. Van Caenegem and D. Haelewaters, unpublished data): four species of *Arthrorhynchus*, two species of *Dimeromyces*, ten species of *Gloeandromyces*, and two species of *Nycteromyces* (**Fig. 8**). In addition, Haelewaters *et al.* (2020) revealed that *Arthrorhynchus eucampsipodae* is a complex of at least two species segregated by host genus. Given that *A. eucampsipodae* has been reported on flies in four genera (de Groot *et al.*, 2020), it could very well be a complex of four species, possibly more.

Some of the Laboulbeniales species associated with bat flies penetrate their hosts with haustoria, rhizoidal structures that make contact with the body cavity for nutrition and as a holdfast. Haustorial Laboulbeniales are those that have recently been referred to as the true biotrophic members of the order (Reboleira *et al.*, 2021). Bat flies with haustorial Laboulbeniales are often deformed and their integument is severely blackened (due to melanization) at the site of infection (Jensen *et al.*, 2019). The extent of damage to the hosts is largely unknown and probably varies among Laboulbeniales (Kaishian *et al.*, 2023). However, Szentiványi *et al.* (2020) showed that *Arthrorhynchus* spp. reduced bat fly survival in *Penicillidia conspiciua* bat flies.

Different studies point at very low parasite prevalences of bat flies with Laboulbeniales, ranging from 2.2% to 9.0% (Blackwell, 1980; Haelewaters *et al.*, 2017a, 2018b; Szentiványi *et al.*, 2018; Walker *et al.*, 2018). Except some regional studies focusing on prevalence of parasites and one study reviewing tritrophic associations globally and analyzing host specificity patterns (de Groot *et al.*, 2020), other aspects remain unstudied. Efforts are being made towards a global tritrophic traits database to study some of these aspects based on records resulting from standardized fieldwork (Haelewaters *et al.*, 2021a). One question of interest is how environmental pressures such as changing landscapes and warming climate affect parasitism at these multiple levels.

Other examples of Laboulbeniales that have parasites as hosts are found in two other genera: *Rickia* on mites of ants, *Salganea* cockroaches, *Nasutitermes* termites, and beetles in different families; and *Trenomycetes* on lice of birds, cows, foxes, and rats as well as on louse flies of primates (*Lepilemur* sp.). In addition, species of *Dimeromyces* are not only associated with bat flies, they are also found on mites of beetles in different families. It should be mentioned that it is not always clear whether these mite hosts are truly parasites or rather commensals in relation to the primary host. Finally, written notes by Jean Balazuc at the Muséum National d'Histoire Naturelle, Paris reveal an unpublished genus of Laboulbeniales from a human ectoparasite (the sucking louse *Pediculus humanus*, order Psocodea).

4.5. Basidiomycetous hyperparasites

Examples of basidiomycetous hyperparasites are surprisingly scarce. Roughly 200 species of mycoparasites have been described in this phylum, with a dozen of them being putative hyperparasites. Examples of hyperparasitism have been documented in four classes: Agaricomycetes, Tremellomycetes (Agaricomycotina), Ustilaginomycetes (Ustilaginomycotina), and Pucciniomycetes (Pucciniomycotina). The best studied group of hyperparasites within Basidiomycota is Helicobasidiales (Pucciniomycetes). This order comprises species of *Tuberculina*, which are hyperparasites of rusts (**4.1.4. Hyperparasites of rusts**). Within Agaricomycetes and Tremellomycetes, evident examples of hyperparasitism are extremely rare, but see **Table 1** for specific examples.

In Agaricomycetes, only two examples of hyperparasitism are known. Both *Collybia cookei* and *Entoloma*

abortivum have been reported as hyperparasites on species of *Armillaria* (Lindner *et al.*, 2001) (**Table 1**). *Armillaria* species are devastating, necrotrophic phytoparasites on various tree species, but may shift to saprotrophism once the host tree has died. Most species within Tremellomycetes are mycoparasites and lichen parasites (Diederich *et al.*, 2022; Millanes *et al.*, 2011; Weiss *et al.*, 2014). However, host species identity is often uncertain (only identified to genus or form group) or not known at all. This makes it very hard to estimate which proportion of these mycoparasites are to be considered hyperparasites. Further, for the majority of these hyperparasites, no cultures nor genetic data are available, and their classification remains tentative based on (micro)morphological similarities (Schoutteten *et al.*, 2023; Weiss *et al.*, 2014).

5. Ecological role of fungal hyperparasitism

Although a common phenomenon in nature, the real impacts of hyperparasitism on the ecology and evolution of the organisms involved and its cascading effects throughout food webs is understudied. In the broad sense, hyperparasites are analogous to predators, where the secondary hosts (primary parasites) act as herbivores and the primary hosts replace primary producers. Therefore, as predators, hyperparasites are able to shape ecosystem stability through top-down cascades (Parratt and Laine, 2016). Hyperparasitic fungi also influence the dynamics of the interactions between the primary hosts and the primary parasites, increase the complexity of the food webs, and play a significant role in regulating population sizes of either partner (Gleason *et al.*, 2014; Sandhu *et al.*, 2021). By decreasing the fitness of their host, hyperparasites may essentially exert a net positive effect on the fitness of the primary host (Northrup *et al.*, 2021; Sandhu *et al.*, 2021). However, a convincing conceptual framework is lacking, and tractable model systems to study hyperparasitic interactions in natural populations are scarce (Péter *et al.*, 2022; Parratt and Laine, 2016).

It is hypothesized that zoosporic parasites have a role in the structure and function of aquatic food webs, by lengthening food chains and carbon paths. As their life cycles are shorter, zoosporic hyperparasites also increase and accelerate the energy flow among trophic levels, by producing biomass in the form of zoospores and zoosporangia that enter the food web contributing different types of energy for predators (Gleason *et al.*, 2014).

The range of interactions among hyperparasites, their hosts (i.e., the secondary hosts), and the primary hosts is wide and complex, and sometimes difficult to establish (Gleason *et al.*, 2014; Kiss, 2001). Studies on host specificity in hyperparasitic fungal systems are scarce (but see Barnett and Lilly, 1958; Jeffries and Young, 1978), and those examining all three trophic levels in the same analysis are even rarer. One recent study analyzed the ecological interactions among the three levels of the multitrophic network among bats, bat flies, and microfungi and found that bat flies are much more host specific at the community-level compared to their Laboulbeniales hyperparasitic fungi (de Groot *et al.*, 2020).

6. Evidence of hyperparasitic interactions

Studies of hyperparasitic interactions between fungi and their hosts have been observed both in the field and by microscopy (Kim and Vujanovic, 2018; Moore *et al.*, 2020; Smith *et al.*, 2008). However, in most cases, the antagonistic activity of the hyperparasite is not evident in the field, and the exact interactions may only be revealed under laboratory conditions, when the cultivation of the hyperparasite is possible or when infected primary and/or secondary hosts can be reared.

The associations of hyperparasites and their hosts can be visualized by molecular techniques that employ expression of fluorescent proteins (Hasan *et al.*, 2022). For example, the gene-encoding green fluorescent protein (GFP) was expressed in *Trichoderma* species, which helped to elucidate their interactions with *Pythium ultimum*, the invasion of the hyphae and sclerotia of *Rhizoctonia solani*, and the penetration of the plant-parasitic nematode *Globodera pallida* (Contina *et al.*, 2017; Lu *et al.*, 2004; Sarrocco *et al.*, 2006). Also, Németh *et al.* (2019) used a GFP marker to visualize the life history strategy of *Ampelomyces quisqualis*.

Hyperparasitic interactions may be assumed if the parasite causes distinctive morphological or physiological alterations of the primary parasite, with the latter showing signs of phenotypic changes, such as deformation of cells, growth impairment, and changes in color (Gams *et al.*, 2004; Jeffries, 1995; Zheng *et al.*, 2017). For example, urediniospores of *Puccinia striiformis* f. sp. *tritici* collapse and lose viability after being colonized by hyphae of *Alternaria alternata* and *Cladosporium cladosporioides* (Zhan *et al.*, 2014; Zheng *et al.*, 2017). Parasitism may also be assumed when parasites affect the reproductive rate of the hosts, e.g., by decreasing levels of sporulation of fungal hosts. This has been observed for hyperparasites of black mildews, powdery mildews, and rusts and smuts (Bermúdez-Cova *et al.*, 2022; Legler *et al.*, 2016; Zhan *et al.*, 2014; Zheng *et al.*, 2017). The incapability of fungi growing on parasites to be cultured on axenic media, i.e., without their hosts, also serves as an indication that they are obligate hyperparasites (Jeffries, 1995).

7. Molecular studies of hyperparasitic fungi

Hyperparasitic fungi belong to different phylogenetic lineages and have different morphologies, and as a result, no specific set of molecular methods has been developed to study hyperparasites. Yet, despite these differences, researchers frequently encounter similar problems when studying them. Some hyperparasites are minute in size and require non-standard micromanipulation techniques. In addition, many have melanin in their cell walls, which provides rigidity but inhibits PCR amplification and the ability to get high quality DNA (Bermúdez-Cova *et al.*, 2022; Eckhart *et al.*, 2000; Haelewaters *et al.*, 2015).

Because they are part of multitrophic networks, it is common to find hyperparasites intermingled with tissue of the primary parasite and other organisms present in a given sample. This makes the isolation of DNA exclusively from the hyperparasite difficult. Moreover, many hyperparasitic fungi are biotrophs and cannot be grown axenically. The hosts themselves may also be biotrophic, further complicating DNA isolation from either partner. These factors have contributed to a lack of reference sequences for taxonomic and systematics research and also have ramifications even for genomics research; for mycoparasitic hyperparasites, *in silico* attempts at de-novo genome sequencing derived from metagenomic data can be unfeasible because the methods used for separation of host and hyperparasite sequences cannot easily discriminate between the two fungi (Quandt *et al.*, 2017).

Due to the challenges described above, publicly accessible databases are notably lacking in their representation of hyperparasites. As an example, in the latest version of the UNITE database (version 9.0, 27 October 2022) (Nilsson *et al.*, 2018), out of almost 8.4 million ITS sequences, there are only 35 of Laboulbeniales—a taxon with over 2,300 described species and many more yet to be described (Haelewaters *et al.*, 2021a). Not all species in this order are hyperparasites, but many of them are, and as UNITE is the primary database used in environmental microbiome studies (Tedersoo *et al.*, 2022), the paucity of taxa that are represented leads to an underreporting of their presence in nature and therefore our understanding of the natural world.

Generalizations about the genetic “toolkit” that hyperparasitic fungi use are difficult if not impossible to make, due to the phylogenetic and morphological diversity of both the primary parasite and the primary host. However, the nature of individual hyperparasitic relationships can and should be investigated. In one such example, Koch and Herr (2021) used transcriptomics (RNA-seq) to examine the differential expression of genes in both the hyperparasite, *Entoloma abortivum*, and its host, a plant-pathogenic *Armillaria*, during their parasitic interaction compared to expression in their respective sporocarps. Transcripts obtained from the interaction interface are mainly from *E. abortivum*, the hyperparasite, and contain genes hypothesized to be involved in mediating recognition of *Armillaria* and detoxification of compounds produced by the pathogen. Modern techniques such as these now allow for examining the nature of the interaction between the hyperparasite, its primary parasite, and the primary host.

8. Hyperparasitic fungi and biological control

Environmental and health concerns caused by the use of chemicals such as fungicides, nematicides, and pesticides have increased the need for alternative measures for the control of pathogens (Moosavi and Zare, 2020; Thambugala *et al.*, 2020). Hyperparasitic fungi play a significant role in controlling pathogens, and they have been used as biological control agents for at least 70 years (Heydari and Pessaraki, 2010; Thambugala *et al.*, 2020). Biocontrol agents represent an alternative to fungicides in disease control (Köhl *et al.*, 2020). The use and utility of biocontrol agents, however, has had limited success (Savita and Sharma, 2019) and more work is needed to fully examine the most appropriate and beneficial applications of specific hyperparasites in biocontrol.

The fungi best studied for their use in biocontrol are species of the genus *Trichoderma* (Brotman *et al.*, 2010; Harman *et al.*, 2004; Motlagh and Samimi, 2013; Reino *et al.*, 2008). Around 90% of fungal biocontrol agents belong to different strains of *Trichoderma*, and currently more than 60% of the effective bio-fungicides are obtained from species of this genus (Abbey *et al.*, 2019; Hermosa *et al.*, 2012). Moosavi and Zare (2020) stated that 25 species of *Trichoderma* have the potential of controlling more than 100 fungal pathogens worldwide. Out of these species, *Trichoderma harzianum* may be considered the most common and commercially developed biocontrol agent used for a wide range of plant-pathogenic fungi. *Trichoderma* species have an antagonistic behavior against bacteria, nematodes, and fungi by inhibiting growth and they may indirectly improve the growth and stress tolerance of the primary plant host (Kumar, 2013; Zhang *et al.*, 2017).

Clonostachys rosea is a hyperparasitic fungus capable of invading various plant-pathogenic fungi, including *Botrytis cinerea*, *Fusarium* spp., *Rhizoctonia solani*, and *Sclerotinia sclerotiorum* (Barnett and Lilly, 1962; Cota *et al.*, 2008; Jensen *et al.*, 2000; Luongo *et al.*, 2005; Rodríguez *et al.*, 2011), with *C. rosea* strain 67-1 being highly efficient for biocontrol (Zhang *et al.*, 2007; Ma *et al.*, 2011; Sun *et al.*, 2018). Hasan *et al.* (2022) showed that the GFP-marked *C. rosea* strain 67-1 exerts antagonistic activities against *B. cinerea* both *in vitro* and on tomato leaves. The hyperparasite is able to penetrate its host, absorb its nutrients, and eventually disintegrate all of its cells.

Ampelomyces quisqualis has been the subject of numerous investigations on biological control of powdery mildews for over 50 years and, along with species of *Trichoderma*, they are the most common biocontrol agents that have reached international markets (Falk *et al.*, 1995a, 1995b; Kiss *et al.*, 2004). Several cross-inoculation experiments, both *in vitro* and in the field (Angeli *et al.*, 2012; Kiss *et al.*, 2011; Legler *et al.*, 2016; Liang *et al.*, 2007; Németh *et al.*, 2021), have shown that species of *Ampelomyces* are not strictly host specific. This has allowed for biocontrol agents composed of a single strain to be applied to a wide range of powdery mildew species (Németh *et al.*, 2021).

A large number of crop plants are infected by parasitic nematodes (Savita and Sharma, 2019). They represent a major threat to crops worldwide, and due to the toxicity of nematicides, new control strategies against nematodes need to be developed (Poveda *et al.*, 2020). Fungi have shown great potential as nematocidal biocontrol agents (Siddiqui and Mahmood, 1996). Important fungi used in biocontrol of nematodes are *Pochonia chlamydosporia* (Sordariomycetes: Hypocreales), *Purpureocillium lilacinum* (Sordariomycetes: Hypocreales), and *Hyalorbilia oviparasitica* (Orbiliomycetes: Orbiliales) (Lysek and Sterba, 1991). Species of *Trichoderma* are also currently being studied as biocontrol agents of parasitic nematodes.

The processes of commercialization and application of fungi as biocontrol of pests have been slow. This is mainly due to diverse fungal performances under variable environmental conditions in the field as well as their host specificity (Thambugala *et al.*, 2020). The development of new formulations of biocontrol fungi with higher degrees of stability and survival is necessary to overcome this problem (Heydari and Pessaraki, 2010). Commercialization of biological control agents is expensive and involves many steps such as isolation in pure culture, the development of a suitable formulation, mass production, testing efficacy of the product, environmental safety matter assessment, among others (Janisiewicz and Korsten, 2002; Montesinos, 2003).

Moreover, the cultivation of hyperparasites is not always possible and therefore the development of biocontrol products from these fungi remains challenging.

9. Future avenues of research

One of the challenges to studying hyperparasitic fungi includes the ability to recognize the morphology and natural history of both the primary host and the primary parasite in their uninfected states. Currently few experts are trained to identify all of the partners in the different trophic levels of hyperparasitic interactions, which explains the paucity of published literature on this topic. While these hyperparasitic fungal systems are potentially diverse, they are largely unexplored. Multitrophic, multiyear, multisite sampling efforts have been proposed to strengthen future analyses on host specificity patterns and community ecology (Cazabonne *et al.*, 2022; de Groot *et al.*, 2020; Haelewaters *et al.*, 2021a).

In addition to the lack of sampling, little attention has been given to the theoretical framework for systems involving hyperparasites (Sandhu *et al.*, 2021). Most of this work has focused on the use of hyperparasitic fungi in biocontrol experiments, directed toward reducing the damage caused by primary parasites (Day, 2002; Rosenheim *et al.*, 1995). It is essential to understand how parasites interact with their own parasites to effectively control infectious diseases (Parratt *et al.*, 2017).

While much is left unknown about hyperparasitic fungi, the presence and expression of secondary metabolite gene clusters (Quandt *et al.*, 2016, 2018) and their antifungal activities (Wang *et al.*, 2016) among many lineages of mycoparasites including hyperparasites are well documented. The advent of genomics has proven that many species and strains have the ability to produce countless compounds whose activities have the potential for myriad biotechnological and pharmaceutical uses (Keller, 2019). Hyperparasites, many mentioned here in this chapter, likely harbor antifungal compounds that have yet to be discovered and described (Kim *et al.*, 2002; Wicklow *et al.*, 1998). Without more work examining hyperparasitic fungi, these compounds and their potential uses will remain unknown.

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