Mycoparasitism in Basidiomycota

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April 23, 2024

Abstract

Among the over 31,000 recognized species within Basidiomycota, approximately 200 are documented as parasites of other fungi, so-called mycoparasites. They exhibit a remarkable diversity in morphological characteristics, host-parasite interaction structures, and phylogenetic affiliations. Mycoparasitism as a trophic strategy in Basidiomycota has received little attention from the mycological community, with most research performed during the last decades of the previous century. These mycoparasites are documented across three subphyla, encompassing 10 different classes, yet a comprehensive understanding of their evolutionary relationships and host-parasite interaction mechanisms remains limited, and much data are scattered in the literature. This chapter aims to systematically outline the various classes of Basidiomycota known to include mycoparasites, elucidating their diversity, host-parasite interface, life cycle, morphology, and systematic classification. To provide a comprehensive overview of current knowledge on basidiomycetous mycoparasitism, we have compiled a catalogue of presumed mycoparasites, detailing available data for each species.

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1. Introduction

Fungi have evolved different strategies to acquire nutrients. Some fungi, like decomposers, are specialised in gaining nutrients from non-living substrates, whereas others are symbiotic and engage in interactions with other living organisms. These interactions can be mutual, neutral, commensal or parasitic, but these should be seen as a dynamic continuum, as the nature of the interaction between organisms may change over time during the interaction process. Parasitic fungi interact with a broad range of host organisms from all major groups of life on Earth, including other fungi. **Mycoparasitism** is the phenomenon in which a fungus directly derives carbohydrates and other nutrients from another living fungus (Jeffries 1995, Kirk et al. 2008). This strategy already existed at least 400M years ago (Krings et al. 2018), and is currently known from representatives of nine fungal phyla, being Rozellomycota, Blastocladiomycota, Zoopagomycota, Mortierellomycota, Kickxellomycota, Mucoromycota, Chytridiomycota, Ascomycota, and Basidiomycota (Naranjo-Ortiz & Gabaldon 2019). The currently known diversity of mycoparasites among Basidiomycota is rather modest compared to the total number of currently described species, although it should be taken into account that for many fungi the trophic strategy is not or incompletely known. Mycoparasites have traditionally received little attention from mycologists, and no up-to-date compilation of the knowledge on basidiomycetous mycoparasite diversity and interaction mechanisms is available.

Any basidiomycetous species that derives carbohydrates and other nutrients from another living fungus, during at least one phase of its life history can be classified as a basidiomycetous mycoparasite (Jeffries & Young 1994). Basidiomycetous mycoparasites are frequently listed as fungicolous fungi, without details on the nature of the interaction between the two species involved. Apart from parasitic interactions, **fungicolous fungi** may potentially engage in commensal, neutral, and even mutualistic relationships. As such, mycoparasites only comprise a subset of fungicolous fungi.

A major obstacle in outlining mycoparasitic Basidiomycota is that the nature of the relationship between two co-occurring fungal species is not easy to determine. Hard evidence for parasitic associations requires insights into nutrient flows between the interaction partners and measuring the effects on the host fitness. Also, obtaining scientific proof of host-parasite associations requires the establishment of reinfection experiments. The parasitic nature of the currently known basidiomycetous mycoparasites is mostly inferred from the presence of specialised host-parasite interaction structures such as haustorial cells. Even when such interaction structures are not observed or reported, mycoparasitic behaviour is attributed to some species because of consistent co-occurring patterns with their host, and/or the fact that morphologically similar or phylogenetically closely related organisms are known as mycoparasites.

Mycoparasites among Basidiomycota comprise a heterogenous, phylogenetically diverse group of fungi, most of them belonging to subphyla Agaricomycotina and Pucciniomycotina (Aime et al. 2014, Weiß et al. 2014). Clear examples of mycoparasitic interactions in Ustilaginomycotina are rare, e.g., Kolařík et al. (2021) introduced Quasiramulariales to accommodate a recently discovered mycoparasite of a phytoparasitic rust fungus. In Pucciniomycotina, mycoparasitism is phylogenetically widely distributed and occurs in at least six out of ten classes, whereas in Agaricomycotina, the majority of mycoparasites is restricted to Tremellomycetes. Only a handful of presumed mycoparasites are known from Agaricomycetes.

Basidiomycetous mycoparasites are generally characterised by minute basidiomes, often growing adjacent to, or closely attached to basidiomes of their host species. **Intrahymenially** growing mycoparasites do not produce own basidiomes, but grow in the tissues of their host (Oberwinkler 1964). When these intrahymenial mycoparasites do not cause visible infection patterns, they can only be visually detected during microscopic investigation of their host. Most basidiomycetous mycoparasites display one or multiple characteristics that are typical for the former Heterobasidiomycetes, namely septate basidia, repetitive spores, capability to revive when rehydrated after a prolonged period of desiccation, and a **dimorphic lifecycle**. To date, it is clear this is not a monophyletic group of organisms, and these characteristics evolved multiple times in several lineages. The concept of dimorphic lifecycles in Basidiomycota was introduced by Brefeld (1888) to comprise heterobasidiomycetes which develop basidiospores able to germinate by yeast-like budding. Such dimorphic heterobasidiomycetes usually alternate between a filamentous morph and a yeast morph, which in most cases correlate with the dikaryotic and haploid stages of the lifecycle, respectively. Conjugation of two compatible yeast cells initiates the transition from the haploid stage to the dikaryotic stage and often initiates a change in ecological strategy. In dimorphic mycoparasites, the yeast morph is considered to be saprobic, whereas the filamentous morph represents the mycoparasitic stage. Mycoparasites with dimorphic lifecycles can be found in several groups of Pucciniomycotina and in Tremellomycetes.

The few basidiomycetous mycoparasites investigated for their ultrastructure using transmission electron microscopy (TEM) revealed the existence of three major types of host-parasite interaction mechanisms: 1. **colacosome interaction** (Cryptomycocolacomycetes and Microbotryomycetes), 2. **nanometer-fusion pore interaction** (nm-fusion; Agaricostilbomycetes, Classiculomycetes, Cystobasidiomycetes, Spiculogloeomycetes, and Tremellomycetes), and 3. **micrometer-fusion pore interaction** (µm-fusion; Pucciniomycetes). A substantial degree of variation occurs within these interaction types, which is further elaborated upon in the discussion of the different classes.

Many basidiomycetous mycoparasites produce **haustorial cells**. These are specialised cells for interacting with a host cell, and can usually be recognised microscopically. Such haustorial cells were first illustrated by Olive (1946), and typically consist of a widened subglobose basal part, and a slender filamentous outgrowth which varies in length and may bifurcate in some species. Often a globular apex can be recognised at the

distal end of the filament, which attaches to the wall of a host cell. This typical shape of haustorial cells is often referred to as **tremelloid haustorial cells** or even **tremelloid haustoria** in mycological literature. In this chapter, we refer to these structures as haustorial cells, while haustoria correspond to globose or otherwise characteristically formed parts of parasite cells inside host cells (Piepenbring 2022). Haustorial cells occur in various genera in Tremellomycetes and different classes of Pucciniomycotina. However, the question of their homology remains to be assessed (Bauer 2004). Bandoni (1995) suggested that species in Basidiomycota characterised by such tremelloid haustorial cells potentially have mycoparasitic capabilities, but evidence for this assumption is lacking. As far as we know, all investigated haustorial-cell-forming mycoparasites engage in nm-fusion pore interaction, but only a minority of them were investigated for their ultrastructure. Bauer & Oberwinkler (1990) were the first to demonstrate the nm-fusion pore interaction in basidiomycetous mycoparasites when investigating the haustorial-cell-forming *Tetragoniomyces uliginosus*. Mycoparasites engaging in fusion pore interaction establish cytoplasmic continuity between their own cells and the host cells. At the contact surface of the haustorial apex and a host hypha, a small membrane-bound channel is formed by the fusion of plasma membranes of host and parasite through a small pore of < 20 nm diameter, establishing a cytoplasmic bridge. It can be hypothesised that these fusion pores play a role in the mycoparasitic interaction and facilitate nutrient transfer.

Most basidiomycetous mycoparasites were discovered and described by a rather small community of mycologists working on heterobasidiomycetes. As a result, our knowledge about these species is mainly restricted to light-microscopy-based morphological observations. Only a few mycoparasites are available in public culture collections and were investigated in detail for their phylogenetic relationships, host-parasite interface, and other relevant ultrastructural properties. The majority of these ultrastructural details for a wide range of species were obtained by the late transmission electron microscopist Dr. Robert Bauer and his collaborators from the former Lehrstuhl für Spezielle Botanik und Mykologie (univ. Tübingen, Germany), headed by the late Prof. Dr. Franz Oberwinkler. Without their contributions, our knowledge about basidiomycete mycoparasitism would be minimal. Since much information on these mycoparasites is dispersed in relatively old literature often hard to access, we believe that a compilation of these taxa and outlining the available information about them is a necessary and worthwhile undertaking. The limited amount of available data and living cultures of mycoparasites impede the outline of an evolutionary framework of this lifestyle strategy in Basidiomycota. Also, elucidation of species boundaries and the establishment of a monophyly-based systematic framework for mycoparasitic taxa remains difficult, just like inferences on host specificity. In this chapter we aim to provide **1) a systematic overview of basidiomycetous mycoparasites**, including information on evolutionary relationships, host, and availability of specific data, and **2) an in-depth discussion of the different classes to which mycoparasites belong**.

2. Compilation of mycoparasitic taxa

Table 1 outlines all presumed mycoparasitic species in Basidiomycota, except for Agaricomycetes. Also, lichenicolous fungi, which in a strict sense can be considered mycoparasites when parasitising the fungal component of the lichen association, are not included in this list and are not discussed in this chapter. Criteria for inclusion in the list were the presence of host-parasite interaction structures, or the presence of a co-occurring presumed host species (as reported in literature). Only formally described species are included. Author names of mycoparasitic taxa are mentioned in the table. The included species are listed in a systematic order, following subphylum, class, order and genus levels. Genera currently classified as *incertae sedis* are listed separately at the end of **Table 1**. We realize that some mycoparasitic species or some of the listed characteristics may be missing, and we welcome readers to inform us about missing data.

The columns in this table are scored as follows:

Sequence data available: We searched for all taxa in literature and GenBank for relevant DNA sequence data, with a primary focus on ribosomal ITS sequences. *Host-parasite interaction mechanism*: Assessment

of the host-parasite interaction mechanism based on original descriptions and later reports of the respective species. We used four different categories: unknown, haustorial cells, micropore fusion, and colacosomes. These categories only reflect the gross morphology of the interaction structures, and a considerable amount of variation occurs in these categories at the ultrastructural level. The presence of haustorial cells and colacosomes was assessed based on descriptions, drawings or pictures available in literature. *Lifecycle*: Knowledge of the different morphs that are known from each species. Since the mycoparasitic stage of the included species generally correlates with the dikaryotic developmental stage and the filamentous morph, the default category is 'Filamentous'. Dimorphic taxa have both a yeast morph and a filamentous morph. Evidence for the presence of a yeast morph comprises the availability of yeast cultures in public collections, or the report of yeast(-like) budding of basidiospores in descriptions, drawings, or pictures of the respective species. *Basidiome*: Assessment of the mycoparasite basidiome morphology. Mycoparasites which do not develop own basidiomes, but grow in the hymenium of other species are categorised as 'Intrahymenial'. *Host*: Host species that are reported in literature for the respective mycoparasite. When multiple hosts are known, all are listed. *Country*: The current nation-state of the type locality of the respective mycoparasite. *Selected references*: For each taxon, at least one relevant reference concerning the host-parasite association is given.

Mycoparasite	Sequence data available	Host-parasite interaction mechanism	Life cycle	Basidiome	Host fungus	Host order	Country of type locality	Selected References
Pucciniomycotina								
Agaricostilbomycetes *Chionosphaera* D.E. Cox								
Chionosphaera phylaciicola (Seifert & Bandoni) R. Kirschner & Oberw.	No	-	Dimorphic	Stilboid	*Phylacia poculiformis* (Kunze) Mont.	Xylariales	Venezuela	Seifert et al. (1992)
Mycogloea L.S. Olive								
Mycogloea amethystina Bandoni	No	-	Filamentous	Pustulate	-	-	Canada	Bandoni (1998a)
Mycogloea bullatospora Bandoni	No	-	Filamentous	Pustulate	-	-	Thailand	Bandoni (1998a)
Mycogloea carnosa L.S. Olive	No	-	Filamentous	Pustulate	-	-	USA	Olive (1950)
Mycogloea macrospora (Berk. & Broome) McNabb	No	-	Filamentous	Pustulate	-	-	Great Britain	Berkeley & Broome (1873)
Mycogloea nipponica Bandoni	Yes	-	Dimorphic	Pustulate	-	-	Japan	Bandoni (1998a); Kirschner et al. (2003)
Mycogloea orthospora (Syd.) McNabb ex Dingley	No	-	Filamentous	Pustulate	-	-	New Zealand	McNabb (1965); Bandoni (1998a)
Mycogloea tahitiensis L.S. Olive	No	-	Filamentous	Pustulate	-	-	French Polynesia	Olive (1958a)
Kondoa Y. Yamada, Nakagawa & I. Banno								
Kondoa myxariophila J.P. Samp., Q.M.	Yes	Haustorial cells	Dimorphic	Only observed	*Myxarium nucleatum* s.l.	Auriculariales	Portugal	Li et al. (2020)

3. General overview of mycoparasitism in Basidiomycota

Our compilation of basidiomycetous mycoparasites in **Table 1** reveals 202 species which are presumed mycoparasites. For less than half of them, namely 94, DNA sequence data are available, implying that for the majority the systematic position remains uncertain. Most of these taxa, e.g., many species in *Achroomyces* and *Tremella*, are currently assigned to a genus based on morphological similarities only. However, it has been shown that several morphological characters formerly used as a base for systematics are plesiomorphic and do not correlate with phylogenetic position (e.g., Millanes et al. 2011), and yet unsequenced species are in need of reinvestigation to achieve a molecular-based systematic arrangement. The lack of genetic data largely correlates with the unavailability of living cultures of a specific species in public culture collections.

For most mycoparasites, the host-parasite interaction mechanism is poorly known. Tremelloid haustorial cells have been mentioned or illustrated in literature for 121 mycoparasites. Detailed TEM studies of a few species with haustorial cells have shown them to engage in nm-fusion pore interaction, but this cannot be extrapolated to all species with haustorial cells without proper investigation. It may be that other, yet undiscovered, interaction mechanisms are present among those species with haustorial cells. Currently, 16 species are recorded as colacosome-interacting mycoparasites (Cryptomycocolacomycetes and Microbotryomycetes), and four species engage in micrometer-fusion pore interaction (Pucciniomycetes). For at least 61 species, the host-parasite interaction mechanism is unknown. It can be assumed that most of these are either nm-fusion pore or colacosome-interacting mycoparasites, but there is a possibility that some species comprise previously undiscovered interaction mechanisms.

Dimorphic lifecycles are known from 104 mycoparasites, whereas 52 species are known from a filamentous morph only. For 44 species we could not retrieve sufficient data to assess the lifecycle. For basidiomycetous mycoparasites, the parasitic stage always correlates with a filamentous morph, but an undetected yeast morph does not imply or prove its absence. Most basidiomycetous mycoparasites produce a certain type of basidiome, but 58 currently known species grow intrahymenially in their host. For the vast majority of basidiomycetous mycoparasites, only one host species has been reported. Host species of basidiomycetous mycoparasites are divided over both Ascomycota (58) and Basidiomycota (98). For 43 mycoparasites, no information is available that allows to assign the host to a specific fungal phylum. In decreasing order, hosts among Ascomycota belong to Xylariales (18 species of mycoparasites), Rhytismatales and Helotiales (each 5), Pleosporales (4), Diaporthales (3), Hypocreales, and Microascales (each 2), Cladosporiales, Coniochaetales, Hysteriales, and Sordariales (each 1). Hosts among Basidiomycota belong to Russulales (23), Hymenochaetales (17), Auriculariales (12), Agaricales (9), Dacrymycetales (8), Cantharellales (7), Polyporales, and Pucciniales (each 5), Corticiales (2), Atractiellales, Boletales, Trechisporales, Tremellales, and Xenasmatellales (each 1). More than half of the mycoparasites are described from Europe (101), followed by North America (36), Asia (32), South America (13), Meso America (9), Pacific Ocean islands (5), Oceania (3), Africa (1), and Atlantic Ocean islands (1).
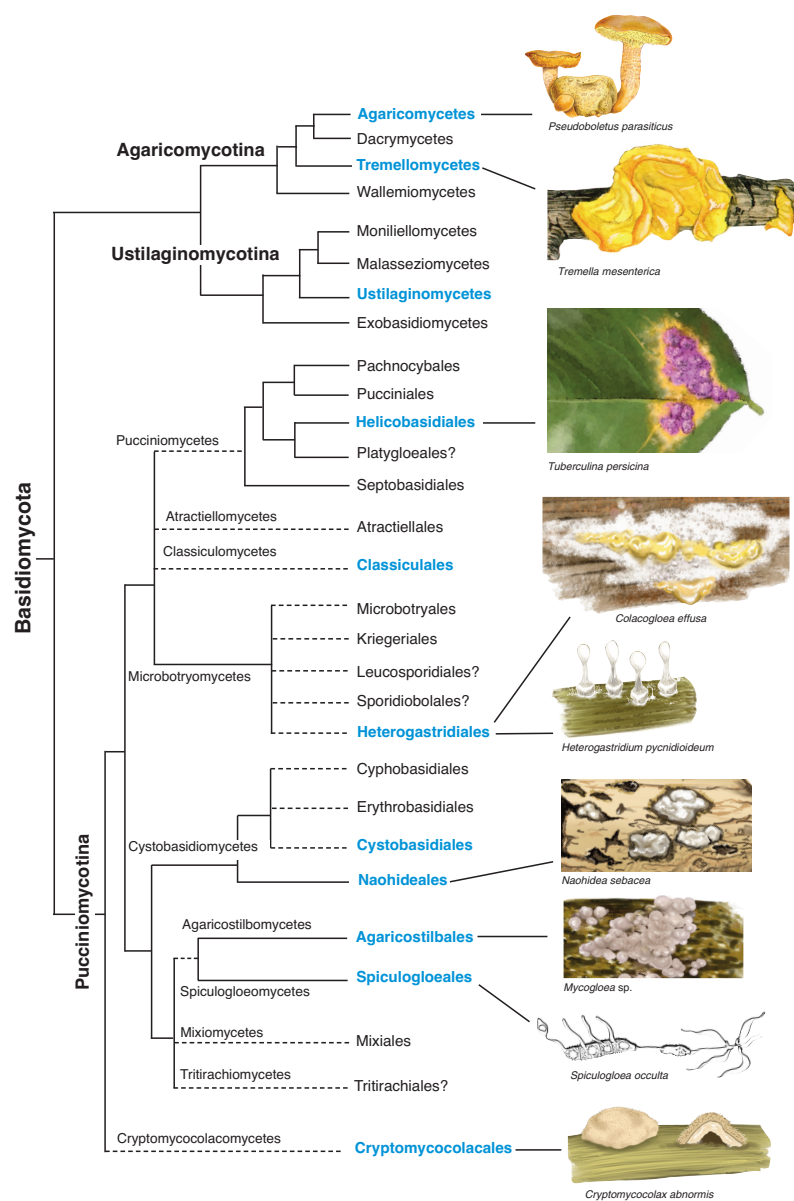
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Figure 1: **Fig. 1. Phylogram of Basidiomycota displaying groups with mycoparasitic species.** Taxa comprising mycoparasites are indicated in blue. For several groups a typical mycoparasite is illustrated. The relationships depicted in this phylogram represent an interpretation based on multiple previously published phylogenetic reconstructions (Aime et al. 2006, Bauer et al. 2006, Wang et al. 2015a) and the phylogenomic relationships as represented in MycoCosm (https://mycocosm.jgi.doe.gov/mycocosm/home). Dashed lines represent uncertain relationships. Question marks indicate groups in which the presence of mycoparasites is suspected.

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4. Discussion of groups in systematic order

4.1 Pucciniomycotina - Agaricostilbomycetes

This class currently comprises six families, with all species characterised by dimorphic lifecycles or known exclusively from yeast morphs. Filamentous morphs with sexual structures were reported from Agaricostilbaceae, Chionosphaeraceae, Crittendeniaceae, and Kondoaceae, whereas in Jianyuniaceae and Ruineniaceae only yeast morphs are known. Sexual structures are characterised by either transversally one- to three septate phragmobasidia (Agaricostilbaceae, Chionosphaeraceae pro parte, and Kondoaceae) or holobasidia (Chionosphaeraceae pro parte, Crittendeniaceae). Sexual structures of Agaricostilbaceae and Chionosphaeraceae are characterised by statismosporic basidia (in older literature also referred to as gasteroid basidia), producing sessile basidiospores. In contrast, sexual structures of Kondoaceae species are characterised by transversally septate ballistosporic basidia, producing actively discharged basidiospores.

In literature, Agaricostilbomycetes are often regarded as lacking haustorial cells (Bauer et al. 2006, Begerow et al. 2018). However, Seifert et al. (1992) reported the development of haustorial cells in *Stilbum vulgare* attaching to hyphae of *Cladosporium* sp. when growing in co-culture. Also, the recent description of *Kondoa myxariophila*, which produces haustorial cells in pure culture, challenges this view (Li et al. 2020). To date, such interaction structures have not yet been reported from natural conditions. Consequently, the ecological strategies of these species in natural conditions remain incompletely known, but it can be assumed that they have mycoparasitic capabilities. Seifert et al. (1992) described the fungicolous *Chionosphaera phylaciicola* growing on ascomata of *Phylacia poculiformis*, but did not report any interaction structures. Various yeast species in the genera *Kondoa* and *Bensingtonia* have been isolated from fruitbodies of other fungi, hinting towards a possible mycophilous relationship. The mycophilous associations of various Agaricostilbomycetes along with the discovery of haustorial cells in two species, hint towards mycoparasitic capabilities for at least some representatives.

Kondoa myxariophila (Kondoaceae) was isolated from basidiomes of *Myxarium nucleatum s.l.*, a species complex that is host to various mycoparasitic Basidiomycota (**Table 1**). *Kondoa myxariophila* is a dimorphic species, characterised by basally clamped haustorial cells and transversally septate basidia producing ballistospores (**Fig. 2D**). The authors indicated that these structures were observed in culture conditions in the absence of mating, and proposed the possibility of a mycoparasitic strategy (Li et al. 2020). Two important questions remain: firstly, do the sexual structures of *K. myxariophila* also develop in natural conditions, thus is it microscopically detectable as an intrahymenial mycoparasite? Secondly, which species of the *M. nucleatum* species complex can be hosts?

Species in the genus ***Mycogloea*** (Chionosphaeraceae) are characterised by small pustulate basidiomes, growing in between or adjacent to fructifications of other fungi (**Figs. 2A, 2C**). Host species comprise both Ascomycota and Basidiomycota, but especially pyrenomycetes. *Mycogloea* species have transversally septate basidia which are described as deciduous, that is, after maturation, basidial cells detach from the probasidium (**Fig. 2B**). Except for *Platygloea pustulata* G.W. Martin & Cain (Pucciniomycetes) and some species of Ustilaginomycetes, especially among species in the genera *Cintractia s.l.*, *Sporisorium*, and *Ustilago* (Piepenbring 2003), detaching basidial cells are restricted to the genus *Mycogloea* and have been interpreted as an adaptation to aquatic dispersal (Bandoni 1998). Currently, seven *Mycogloea* species have been described from different regions in the world (**Table 1**), and all are assigned to the genus based on the presence of pustulate basidiomes and morphological similarities of the basidia (Bandoni 1998). All species have been described in association with other fungi, especially pyrenomycetes, although no haustorial cells or other interaction structures were reported in original literature (Olive 1950, Bandoni 1998, Kirschner et al. 2002). Due to their association with other fungal species, *Mycogloea* spp. are generally considered mycophilous Basidiomycota. Currently, only *Mycogloea nipponica* (**Fig. 2B**) has been cultivated, sequenced, and investigated for its ultrastructural characteristics (Kirschner et al. 2002). A dimorphic lifecycle was observed for *M. nipponica* only, the other species are only known from the filamentous morph. No sequence data are available for the other species, including the type species of the genus, *M. carnosa* L.S. Olive (**Fig.

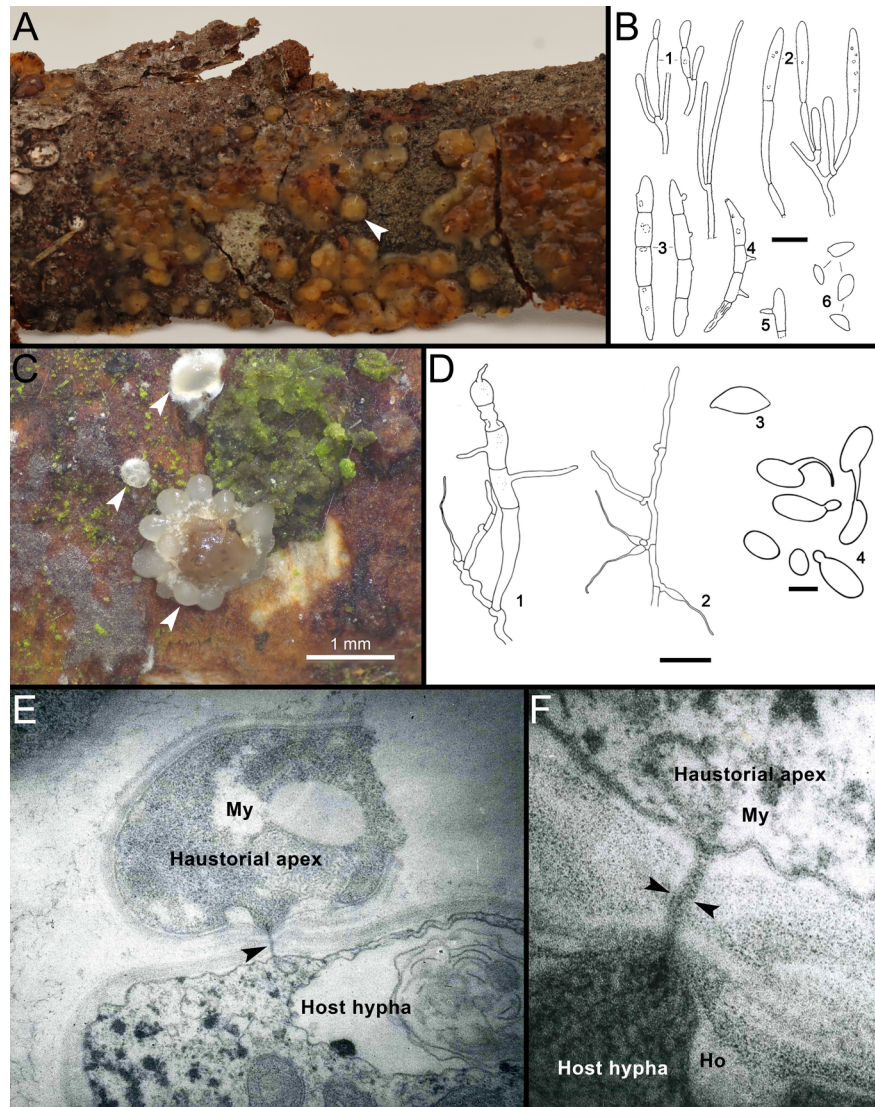**2A**), and it remains to be proven that all species are congeneric.

Figure 2: **Fig. 2. Mycoparasites in Agaricostilbomycetes. A.** Basidiomes of *Mycogloea carnosa* type specimen, pustules (arrowhead) overgrowing the pyrenomycetous host; © Nathan Schoutteten. **B.** Microscopic structures of *Mycogloea nipponica* type specimen; reproduced and modified with permission from Bandoni (1998). **C.** Basidiomes of *Mycogloea* sp., pustules (arrowheads) growing on the basidiome of its host *Peniophora lycii*; © Ida Nannenga-Bruggeman. **D.** Line drawing of microscopic structures of *Kondoa myxariophila*, as obtained in culture, 1: transversally septate basidium with clamped haustorial cell; 2: Hyphae and clamped haustorial cells; 3: basidiospore; 4: yeast propagation and ballistoconidia; reproduced and modified with permission from Li et al. (2020). Scale bars = 10 μm. **E, F.** TEM of cross-section of the host-parasite interface of *Mycogloea* sp. (My) (specimen FO 40962) and its unidentified host (Ho). A haustorial apex is attached to a host hypha and a nm-fusion pore channel (arrowheads) connects the cytoplasms of host cell and parasite cell.

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4.2 Pucciniomycotina - Classiculomycetes

Classiculomycetes are a small class of Basidiomycota, currently only comprising two genera and three species, isolated from aquatic environments in Asia, Europe, and North America (**Table 1**). All species are characterised by navicular conidia with three or four setose branches, the lack of a yeast morph, and the presence of clamped haustorial cells. A sexual stage is known only for *Classicula fluitans*, characterised by transversally three-septate basidia producing ballistospores. Basidia were only observed in pure culture, after soaking the culture in water. All three species are characterised by clamped haustorial cells, consisting of a somewhat thickened basal part with one or multiple filamentous outgrows, which occur at the top or occasionally at the base of the haustorial cell. These outgrows may reach up to 20 μm in length and bifurcation has been observed occasionally. Bauer et al. (2006) reported the attachment of these filamentous outgrows to hyphae of the own mycelium, and interpreted this as *self-parasitism*, possibly being a mechanism to redistribute nutrients in the own mycelium.

Haustorial cells of *Classicula fluitans* were investigated in more detail by Bauer et al. (2003) and were found to be dikaryotic. At the contact interface of the haustorial cell and the invaded hypha, the haustorial apex invaginates the host hyphal cell and is separated by a secondary cell wall layer formed by the invaded host hypha (Bauer et al. 2003). Interestingly, no specific host-parasite interaction mechanism was reported and it is still unknown whether these haustoria engage in fusion interaction or another type of interaction mechanism. Based on morphological similarities of these haustorial cells with those found in other groups of Pucciniomycotina, Bauer et al. (2006) suggested nm-fusion pore interaction for Classiculomycetes, but this remains to be proven. For none of these three species, a host fungus is known and no direct contact has been observed with a possible host species. Despite the lack of knowledge about host species, mycoparasitism, or at least the potential to act as such, has been put forward for Classiculomycetes (Marvanová & Bandoni 1987, Bauer et al. 2003, Bauer et al. 2006).

4.3 Pucciniomycotina - Cryptomycocolacomycetes

Cryptomycocolacomycetes currently comprise the two monotypic genera *Colacosiphon* and *Cryptomycocolax*, comprising two species that are presumed mycoparasites engaging in colacosome interaction. Both species display reproductive structures considered unique among Basidiomycota, and the septal pore complexes are reminiscent of those found in Ascomycota. Because of these deviating characters, we elaborate on these two species in detail.

Cryptomycocolax abnormis was collected in Costa Rica as a gelatinous fungus overgrowing an unidentified ascomycete (**Fig. 3A**) on decaying stems of the herb *Cirsium subcoriaceum* (Asteraceae) (Oberwinkler & Bauer 1990). Reproductive structures (**Fig. 3B**) in this species are unique in Basidiomycota and were interpreted by Oberwinkler and Bauer (1990) as follows: The first meiotic division occurs in a subulate basidial mother cell, resulting in two daughter nuclei that separate in a basal basidial cell and an upper basidial cell, separated by a transverse septum. During this stage, the basidium corresponds to a phragmobasidium. Subsequently, the upper basidial cell is abscised, and its further function is unknown. It is also unknown whether a second meiotic division takes place in this cell. In the basal basidial cell, a second meiotic division takes place, after which the cell elongates up to 100 μm, and statismosporic basidiospores are produced in a successive manner. Yeast budding of basidiospores was observed in microscopic preparations of the basidiomes of *Cr. abnormis*, although basidiospores on MYP and water-agar germinated with clamped hyphae. No living cultures are currently available, and the fungus needs to be recollected for further studies.

The host-parasite interaction is characterised by the presence of colacosomes, which are formed by *Cr. abnormis* along the contact interface with its host cell. Two distinct types of colacosomes were reported for this species, indicated as type-1 and type-2 colacosomes, which is a unique feature among Basidiomycota. The distinction of these two colacosome types is mainly based on morphological differences as observed by TEM, and the location where they are found. Functional inferences of these structures are still hypothetical,

and research is needed to gain more insight into their biochemical composition and function. Contrary to the situation in nm-fusion pore and μm-fusion pore interacting mycoparasites, a cytoplasmic connection between host and parasite has not been observed in any colacosome-interacting mycoparasite.

Type-1 colacosomes are characterised by a globular electron-dense core surrounded by a tripartite membrane and an electron transparent sheet surrounding the core (**Fig. 3D**). This layer is surrounded by a secondary cell wall of the mycoparasite. This complete structure is eventually surrounded by the plasmalemma of the mycoparasite. Sometimes, a tube-like projection of the electron-dense core is formed, breaking through the electron transparent sheet and the cell wall of the mycoparasite and, eventually, the cell wall of the host. Type-1 colacosomes are mainly found at contact surfaces of touching host and parasite hyphae, where no special extensions of host hyphae in the parasite hyphae are formed. This type of colacosomes is also found in *Colacosiphon* (Cryptomycocolacomycetes) and colacosome-forming Microbotryomycetes. Type-2 colacosomes are unique to *Cr. abnormis* (**Fig. 3E**). This type of colacosomes is characterised by a more electron-transparent core compared to type-1 colacosomes. The core is surrounded by a membrane that fuses with the plasmalemma of the attached host hyphae, by means of a small pore of 7–14 nm diameter, formed between the colacosome core and the host cytoplasm (**Fig. 3E**).

Type-2 colacosomes are mainly found surrounding intrusions of host hyphae into invaginations of the mycoparasite hyphal cell (**Fig. 3F**). These intrusions of host hyphal cells in parasite cells lack cell walls, probably facilitating formation of pores connecting host cytoplasm and colacosome cores. Parasite hyphae do have cell walls in these intruded areas, which have to be perforated by the colacosomes to establish pore formation. The dense formation of colacosomes surrounding such invaginated areas results in botryose structures in the mycoparasite cell (**Fig. 3C**), as seen in brightfield- and phase-contrast microscopy (Oberwinkler & Bauer 1990). Note that similar botryose structures are also found in *Colacosiphon* (Cryptomycocolacomycetes) and several colacosome-forming mycoparasites in Microbotryomycetes, although these are formed by type-1 colacosomes without exceptions.

In later stages of the infection process, the cytoplasm of host hyphae that are connected to colacosomes from the attaching mycoparasite hypha will finally become electron-dense, which is interpreted as degeneration. Colacosomes are also formed between appressed hyphae of the mycoparasite itself. Can this phenomenon also be interpreted as self-parasitism as observed in some haustorial-cell-forming mycoparasites? To date, it remains unclear what the exact function of colacosomes is, and if and how the transfer of nutrients to the mycoparasite is established. It remains unknown what the functional difference between type-1 and type-2 colacosomes is. A hypothesis was raised by Bauer et al. (2006), stating that the type-2 colacosome, which produces a nanopore and becomes continuous with the host cytoplasm, may be the ancestral state of the interaction found in nm-fusion pore interacting mycoparasites.

Colacosiphon filiformis is the second species assigned to this class. It was only observed in mixed cultures obtained from bark beetles (*Ips sexdentatus*) collected from felled *Pinus sylvestris* trunks in Germany (Kirschner et al. 2001a). Attempts to further isolate this mycoparasite in pure culture by spore transfer failed, possibly due to host dependency for spore germination. This species differs from *Cr. abnormis* by the absence of both clamps and a phragmobasidial stage. Reproductive structures are strongly deviating from those known in other Basidiomycota, consisting of aseptate sporogenous cells reaching up to 870 μm and apically producing spores (**Fig. 3G**). Kirschner et al. (2001a) argued that it was difficult to interpret the nature of the nuclear divisions in these sporogenous cells due to their rapid development. Due to the deviating morphology of these structures compared to basidia of other Basidiomycota, they were interpreted as conidiophores, although with some reservation (Kirschner et al. 2001a).

Although the identity of the host species remained unclear, Kirschner et al. (2001a) were able to assign it to Ascomycota based on the ultrastructure of the host cell wall. As observed in *Cr. abnormis*, the ascomycetous host produces hyphae which invaginate mycoparasite hyphae (**Fig. 3H**). Colacosomes are produced in the invaginated mycoparasite hyphae along the contact surface of these intrusions (**Fig. 3H, 3I**). *Co. filiformis* is characterised by only one type of colacosomes, namely type-1 colacosomes as observed in *Cr. abnormis*.

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Cryptomycocolax and *Colacosiphon* share some ultrastructural characteristics deviating from those of other Basidiomycota and even show some similarities with the ultrastructure of Ascomycota. The spindle pole body (SPB) morphology and behaviour of *Cryptomycocolax* have intermediate properties between those from Ascomycota and Basidiomycota, but it should be noted that only few species were studied for this character. The SPB discs are large compared to other Basidiomycota, they are inserted in a small pore of the nuclear envelope during the interphase of nuclear division (similar to Ascomycota) and duplicate by splitting of discs during interphase (similar to Ascomycota; Oberwinkler & Bauer 1990, Weiß et al. 2004, Bauer et al. 2006). Unfortunately, SPB properties of *Colacosiphon* have not been investigated in sufficient detail to make comparisons between these two species (Bauer et al. 2006). The area around the septal pores of *Cryptomycocolax* and *Colacosiphon* is devoid of cell organelles and is surrounded by microbodies and Woronin body-like structures. These Woronin-like bodies are similar to those found in Pezizomycotina (Ascomycota). No similar structures in other Basidiomycota representatives are currently known.

These ultrastructural observations have led to the hypothesis that Cryptomycocolacomycetes are an early diverging lineage of Basidiomycota (Oberwinkler & Bauer 1990). This hypothesis was tested with molecular sequence data by various authors (Weiß et al. 2004, Bauer et al. 2006, Aime et al. 2006). However, none of these studies could resolve the phylogenetic position of Cryptomycocolacomycetes, with bootstrap values always lower than 60%. For both species, sequence data are only available for the D1/D2 region of the large subunit rDNA, seriously impeding inferences of evolutionary relationships. Bauer et al. (2006) reported the clustering of *Cryptomycocolax* and *Colacosiphon* on two long branches with high support (100%), although the higher systematic arrangement of the clade remained unresolved. Sampaio et al. (2004a) proposed a possible sister relationship between Cryptomycocolacomycetes and Microbotryomycetes based on the presence of colacosomes in both groups. Ultrastructural properties of septal pore complexes and SPBs separate both groups.
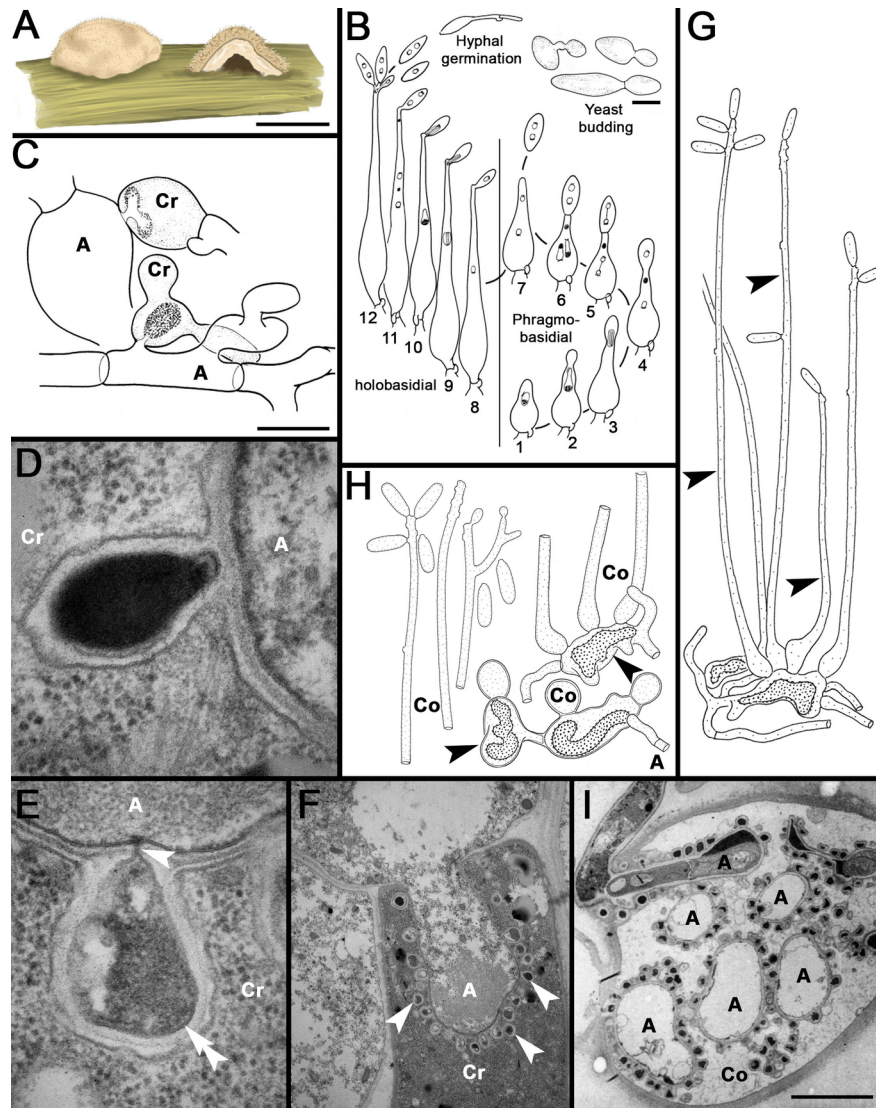
Figure 3: **Fig. 3. Mycoparasites in Cryptomycocolacomycetes. A–F.** *Cryptomycocolax abnormis* **(Cr) with ascomycetous host (A). A.** Habitus of *Cryptomycocolax abnormis* overgrowing its pyrenomycetous host. Scale bar = 1 mm. ⓒ Nathan Schoutteten. **B.** Spore germination and basidial development, stages 1-7 (right of the vertical line) represent the phragmobasidial stage, stages 8-12 (left of vertical line) represent the holobasidial stage. **C.** Host-parasite interface showing host cells (A) invaginating enlarged cells of the mycoparasite (Cr). Along the contact surface, the colacosomes are formed, visible as botryose structures. Scale bar = 10 μm. B, C reproduced and modified from Oberwinkler & Bauer (1990) *Cryptomycocolax*: A New Mycoparasitic Heterobasidiomycete. Mycologia, 82(6): 671-692. Copyright ⓒ1990 The Mycological Society of America, reprinted by permission of Taylor & Francis Ltd, https://www.tandfonline.com on behalf of The Mycological Society of America. **D.** TEM of section through a type-1 colacosome, × 85000. **E.** TEM of a section through a type-2 colacosome. The host plasmamembrane is fused with the membrane surrounding the core of the colacosome (double arrowhead) through a pore (arrowhead), × 85000. **F.** TEM showing a hyphal gall of the mycoparasites that is invaginated by a host hyphae. The host hyphae lacks a cell wall in the invaginating part of the hyphae. Type-2 colacosomes surround the contact surface of the gall and the invaginating host hyphae, × 7000. **G–I.** *Colacosiphon filiformis* **(Co) with ascomycetous host (A). G.** Habitus of *Colacosiphon filiformis* in coculture with its host fungus, note the long sporogenous cells (arrowheads) with swollen basal parts. **H.** Gall hyphae of the mycoparasite in which colacosomes (arrowhead) are formed surrounding the invaginating host hyphae. The gall hypha gives rise to chlamydospore-like cells. G, H modified with permission from Seifert et al. (2011) The Genera of the Hyphomycetes, ⓒ Westerdijk Institute, Netherlands. **I.** TEM showing a hyphal gall of the mycoparasite that is invaginated by a host hyphae. Type-1 colacosomes surround the contact surface of the gall and the invaginating host hyphae. Scale bar = 4 μm. Reproduced and modified from Kirschner et al. (2001) *Colacosiphon*: a new genus described for a mycoparasitic fungus. Mycologia, 93(4): 634-644. Copyright ⓒ2001 The Mycological Society of America, reprinted by permission of Taylor & Francis Ltd, https://www.tandfonline.com on behalf of The Mycological Society of America.

4.4 Pucciniomycotina - Cystobasidiomycetes

Cystobasidiomycetes comprise a heterogeneous group of species, most of them only known from a yeast morph (Begerow et al. 2018). Only a few species are known to have dimorphic lifecycles, of which the sexual stage is characterised by either transversally septate basidia or holobasidia. Species in Cystobasidiomycetes lack fucose in their cell wall carbohydrate composition and yeast morphs often contain carotenoid pigments (Bauer et al. 2006, Begerow et al. 2018). At the ultrastructural level, some dimorphic Cystobasidiomycetes are characterised by septal pores with an apparent simple morphology, each surrounded by a special reticulate pore-occluding structure, referred to as cystosome (**Fig. 4C**) (Bauer et al. 2006). Mycoparasitic species occur in two of the three orders, namely Cystobasidiales and the monotypic Naohideales. All currently known cystobasidiomycete mycoparasites engage in nm-fusion pore interaction enabled by haustorial cells, although there are notable differences between the interaction types of Cystobasidiales and Naohideales at the ultrastructural level.

Cystobasidales

Cystobasidium fimetarium is characterised by purplish pustular basidiomes developing on faeces of different herbivores such as cow dung, rabbit dung, and goat dung (**Fig. 4A**) (Roberts 1999). The lifecycle of *C. fimetarium* is dimorphic, with a haploid yeast morph producing slimy pinkish colonies. The filamentous morph produces sexual structures, characterised by transversally septate basidia arising from thin-walled probasidia, producing ballistospores (**Fig. 4B**). No conidial stage is known from this species. The host-parasite interaction is a nm-fusion pore interaction, with basally clamped haustorial cells attaching to hyphae of the host. In the haustorial apex, a nanopore is formed to establish cytoplasmic contact with the host species (Bauer 2004). *Cystobasidium fimetarium* often grows together with different fimicolous ascomycete genera such as *Ascobolus* Pers., *Lasiobolus* Sacc., and *Thelebolus* Tode, as identified by characteristic reproductive structures. It is assumed that one or several species of these genera act as host species of *C. fimetarium*, although no unambiguous data revealing host identity exists so far. The successive nature of fimicolous fungi may impede unravelling of the identity of the host species. Although only one or a few species may produce reproductive structures at the same time as *C. fimetarium* develops basidiomes, mycelium of other fimicolous species, which are not producing reproductive structures at the same time, may be present in the substrate, and serve as a host for *C. fimetarium*.

The genus ***Occultifur*** was established by Oberwinkler (1990) to accommodate ***Occultifur internus***, an intrahymenial mycoparasite growing in basidiomes of *Dacrymyces stillatus s.l.* The species seems to develop in older, decaying, basidiomes of the host (N. Schoutteten, pers. obs.). Usually, no macroscopically visible signs of infection are visible. *O. internus* is characterised by transversally three-septate basidia producing ballistospores, the absence of distinct probasidia, the presence of conidiophores and ovoid, thick-walled conidia formed with a basal clamp connection, clamped hyphae and the presence of basally clamped haustorial cells (**Fig. 4F**). The haustorial cells of *O. internus* are of the tremelloid type, with a slightly widened basal part, a filamentous outgrowth and a globular apex (**Fig. 4E**). The host-parasite interaction mechanism was interpreted as nm-fusion pore interaction by Bauer et al. (2006). Haustorial cells attach with their apex to the hyphae of the host, and a nanopore is formed to establish cytoplasmic contact between both species (**Fig. 4G**) (Weiß et al. 2004, Bauer 2004, Bauer et al. 2006, Oberwinkler & Bauer 2018). Currently, no cultures or DNA sequence data are available for this species.

Occultifur externus is a dimorphic species isolated from plant litter in Portugal (Sampaio et al. 1999). The sexual stage is characterised by transversally three-septate basidia producing ballistospores, conidiophores producing thin-walled conidia, clamped hyphae and basally clamped haustorial cells. The sexual morph was observed in pure culture only (Sampaio et al. 1999), and it remains unclear whether it concerns a mycoparasite, and if so, what the identity of the host species is. Contrary to *O. internus*, for *O. externus* a culture and DNA sequence data are available. The species was assigned to Cystobasidiomycetes with high

support in different studies (Sampaio et al. 1999, Weiß et al. 2004, Bauer et al. 2006, Aime et al. 2006, Wang et al. 2015a,b).

Since no DNA sequence data are currently available for *O. internus*, the type species of the genus, the assignment of the genus *Occultifur* to Cystobasidiomycetes has not yet been confirmed by molecular phylogenetic analysis. The tentative placement of *Occultifur* in Cystobasidiomycetes is based on similarities in the ultrastructure of the septal pore apparatus of *O. internus* and *O. externus*, which both contain **cystosomes** (Sampaio et al. 1999, Weiß et al. 2004, Bauer et al. 2006, Oberwinkler & Bauer 2018). Cystosomes were also reported from *C. fimetarium* (**Fig. 4C**), indicating the cystosome may be a synapomorphy of species in Cystobasidiales. However, the function of this peculiar organelle is still unknown. Four more presumably mycoparasitic species were assigned to the genera *Cystobasidum* and *Occultifur* based on micromorphological similarities: *Cystobasidium sebaceum*, *C. proliferans*, *Occultifur corticiorum*, and *O. rivoirei*. However, no DNA sequence data or ultrastructural data are available and it is questionable that these species have affinity to Cystobasidiomycetes. Schoutteten et al. (2023) suggested that *C. sebaceum* is most likely a member of the genus *Slooffia* (Microbotryomycetes).

Naohideales

Naohideales are a monotypic order, established to accommodate **Naohidea sebacea**, a dimorphic mycoparasitic species growing on pyrenomycetes (Oberwinkler 1990). This species forms basidiomes that are visible as a gelatinous layer of anastomosing pustules overgrowing stromata of the host species (**Fig. 4H**). Micromorphologically, the species is characterised by stalked, transversally three-septate basidia, absence of a distinct probasidium, absence of conidiophores and conidia, clamped hyphae, and intracellular haustoria (**Fig. 4I**). The basidia of this species are exceptionally long compared to those of other basidiomycetous mycoparasites, reaching up to 275 µm in length. Basidia produce ballistospores on sterigmata which may be bifurcating in some cases. In old or very wet basidiomes statismospores may be formed, directly budding off from basidial cells (Oberwinkler 1990). In the latter case, the spores are formed internally in basidial and occasionally hyphal cells, after which they budd off from special budding loci. Oberwinkler (1990) called these spores endospore-like cells. The compartments in basidia or hyphal cells containing endospores are separated by clampless septa. Basidiospores can form secondary spores and germinate by budding off yeast cells. Contrary to the typical pinkish-orange colonies of yeast forming Cystobasidiomycetes, *N. sebacea* yeast colonies are cream-coloured. Ultrastructurally, this species is characterised by simple septal pores without cystosomes. *N. sebacea* displays a type of host-parasite interaction unique to Basidiomycota. Haustoria of *N. sebacea* almost completely penetrate host hyphae. Penetrating haustoria are surrounded by an electron transparent layer that separates the haustorium from the host cytoplasm. In the region of the haustorial apex, several membrane-bounded fusion pores are formed traversing the electron transparent layer surrounding the haustorial apex and connecting the host and mycoparasite cytoplasm (**Fig. 4J**). Because of the nm-size diameter range of these fusion bridges, this type of interaction is interpreted as nm-fusion pore interaction (Bauer 2004, Bauer et al. 2006).

Figure 4: **Fig. 4. Mycoparasites in Cystobasidiomycetes**. **A–C.** *Cystobasidium fimetarium*. **A.** Basidomata of *C. fimetarium* developing on rabbit dung, no host fructifications are visible (specimen DMS-10172393); © Nathan Schoutteten. **B.** Microscopic structures of *C. fimetarium*; original drawing by F. Oberwinkler. Scale bar = 20 μm. **C.** TEM showing section through a septal pore of *C. fimetarium*, which is occluded by a cystosome (arrowhead). Scale bar = 0.2 μm. **D–G.** *Occultifur internus*. **D.** Basidiome of *Dacrymyces* cf. *stillatus* infected with *Occultifur internus*; © Roeland Enzlin. **E.** Epifluorescence microscopy of Congo-red stained sample of *O. internus*, showing conidiophores and haustorial cells (arrowheads) attaching to host hyphae (specimen NS 20-130B); © Nathan Schoutteten. **F.** Microscopic structures of *O. internus;* original drawings by F. Oberwinkler. **G.** TEM of cross-section of the host-parasite interface of *O. internus* (O) (specimen FO31775) and *Dacrymyces* cf. *stillatus* (D). Haustorial apex attached to a host hypha and a nm-fusion pore (arrowheads) connects the cytoplasms of host cell and parasite cell, × 50000. **H–J.** *Naohidea sebacea*. **H.** Basidiome of *N. sebacea* overgrowing its pyrenomycetous host (specimen ID 7630); © Nathan Schoutteten. **I.** Microscopic structures of *N. sebacea*; original drawing by F. Oberwinkler. Scale bar = 20 μm. **J.** TEM of section through haustorial apex of *N. sebacea*, showing five nm-fusion pores (arrowheads) connecting the cytoplasm of the ascomycetous host (A) and mycoparasite (N), × 5085.

4.5 Pucciniomycotina - Microbotryomycetes

Microbotryomycetes constitute the second largest class of Pucciniomycotina after Pucciniomycetes, with currently seven described orders and more than 300 described species (Begerow et al. 2018, Li et al. 2020, Cao et al. 2021). This class is one of the ecologically and morphologically most diverse groups of the subphylum Pucciniomycotina, and currently, there is no character unifying all members of the class, except for molecular DNA sequence data. The most species-rich group (> 150 spp.) comprises the dimorphic phytoparasites belonging to the Microbotryales, including the anther smuts. A second important ecological group in this class comprises mycoparasites, which all share the *colacosome interaction* type (Bauer 2004, Bauer et al. 2006). Most mycoparasites in this class have originally been described morphologically only and were later assigned to Microbotryomycetes based on the presence of colacosomes or molecular phylogenetic reconstructions. For a few mycoparasites, no cultures and/or DNA sequence data are available, so their placement in this class is still tentative. Most mycoparasites are dimorphic species, including a haploid yeast morph. However, there are some notable exceptions such as *Hyalopycnis blepharistoma* (Berk.) Seeler, a colacosome-interacting mycoparasite known from a filamentous morph only. A third group of species comprises a phylogenetically diverse group of Microbotryomycetes which are known from a yeast morph only, but some of them are able to complete their lifecycle under laboratory conditions in pure culture after mating with compatible yeast cells. These organisms have been isolated from a large variety of regions (tropical to (ant)arctic regions), environments (aquatic, marine and terrestrial) and substrates (soil, streams, phylloplanes, lichens,...). The ecological relevance and interactions for most of these yeast species remain elusive (Begerow et al. 2017, 2018). Some of these species develop a filamentous morph with sexual structures in pure culture and were found to produce colacosomes in their hyphae. This indicates a possible mycoparasitic strategy for these fungi, although no interactions with other fungal species have been observed (Boekhout et al. 1992, Sampaio et al. 2003, Oberwinkler 2017, Begerow et al. 2018). The wide phylogenetic distribution of colacosome-forming species indicates that the ancestor of Microbotryomycetes probably was a colacosome-interacting mycoparasite, and that the ability to form colacosomes was lost multiple times during the course of evolution (Bauer et al. 2006). A shift towards phytoparasitism has occurred at least twice, once in Microbotryales and once in the lineage of *Kriegeria eriophori* Bres. All phytoparasitic species have a haploid yeast morph in their lifecycle and are devoid of colacosomes (Bauer et al. 2006).

Colacosomes in Microbotryomycetes are **restricted to type-1 colacosomes** also known from Cryptomyco-colacomycetes (see above). For the first time, they were reported by Kreger-van Rij & Veenhuis (1971), who observed these subcellular structures in hyphae of four species originally referred to as 'red yeasts': *Rhodosporidiobolus ruineniae*, *Sporobolomyces johnsonii*, *Sporobolomyces salmonicolor*, and *Rhodotorula toruloides*. The authors referred to these structures as *lenticular bodies* but did not speculate about their function. Bauer & Oberwinkler (1991) discovered similar subcellular structures along the contact surface of *Colacogloea effusa* [as *Platygloea peniophorae*] and its host *Peniophorella praetermissa*, and introduced the term colacosomes. The authors suggested that colacosomes are involved in the mycoparasitic behaviour of *Colacogloea effusa* on its host *Peniophorella praetermissa*. Meanwhile, colacosomes have been observed in hyphae of members of Heterogastridiales, Leucosporidiales and Sporidiobolales. All filamentous microbotryomycetous mycoparasites isolated from a host fungus are tentatively placed in Heterogastridiales, but a recent study showed that this needs to be revised. The role of colacosomes in species of Leucosporidiales and Sporidiobolales remains to be determined, but the capability to engage in mycoparasitic interactions cannot be ruled out.

At least **four different types of colacosome arrangement** are currently known in microbotryomycetous mycoparasites (Bauer 2004, Schoutteten et al. 2023). The first type is characterised by a more or less linear placement of colacosomes, where colacosomes are formed along the contact surface of host and parasite hyphae. This organisation type is found in *Colacogloea effusa*, but it also occurs in species characterised by additional colacosome arrangement types as described below. A second type is characterised by formation of galloid cells of the parasite, which are invaginated by outgrows of host hyphae (**Figs. 5B, 5E**). Along the contact surface, numerous colacosomes are formed and the host cell often lacks a cell wall in these

intrusions. Due to the dense arrangement of colacosomes, these intrusions are often visible as botryose structures in light and phase contrast microscopy, similar to those observed in Cryptomycocolacomycetes (**Figs. 3C, 3F, 3H, 3I**). This organisation type has been found in various species such as *Colacogloea bettinae*, *Krieglsteinera lasiosphaeriae* and *Hyalopycnis blepharistoma*. A third type is recognised as a regular placement of colacosomes in parasite hyphae coiling around host hyphae. So far, this type of arrangement has only been found in *Colacogloea papilionacea* and *Slooffia micra* (Kirschner & Oberwinkler 2001, Schoutteten et al. 2023). A fourth type has been observed by Bauer (2004) in a yet undescribed colacosome-interacting mycoparasite of a *Tulasnella* host. The mycoparasite was preliminary named '*Mycospira*', but has not been formally described. For this arrangement type, it has been hypothesised that the mycoparasite forces its host to spirally grow around mycoparasite hyphae. At regular distances, individual colacosomes are formed by the mycoparasite.

Heterogastridiales

Hyalopycnis blepharistoma, a highly peculiar mycoparasite producing pycnidioid basidiomes (**Figs. 5F, 5G**), is one of the few species in Microbotryomycetes apparently lacking a yeast morph in its lifecycle. Interpreted as an ascomycetous fungus for a long time, the basidiomycetous nature of this species has been recognised by Bandoni & Oberwinkler (1981), who detected clamp connections in the anamorphic state of this fungus. The sexual state was observed nine years later by Oberwinkler et al. (1990b), who established the name *Heterogastridium pycnidioideum* Oberw. & R. Bauer for the sexual morph, as well as the family Heterogastridiaceae, and the order Heterogastridiales to accommodate this species. According to the one fungus = one name principle, *Heterogastridium pycnidioideum* is to be considered as a synonym of *Hyalopycnis blepharistoma* (Aime et al. 2018). *H. blepharistoma* is characterised by pycnidioid basidiomes, transversally three-septate basidia producing statismospores with four radiating branches, presence of conidiophores and conidia, and clamped hyphae (**Fig. 5F**). Mature basidiospores accumulate at the top of the pycnidium in a slimy droplet (**Fig. 5G**), which could be an adaptation to animal dispersal. The colacosome interaction along the host-parasite interface was reported by Bauer (2004). In pure culture, this species develops colacosomes along touching hyphae of its own mycelium (Teun Boekhout, pers. comm.). *Hyalopycnis blepharistoma* seems to have a broad host range, with reported host species from both Ascomycota and Basidiomycota (Bandoni & Oberwinkler 1981, Begerow et al. 2018). The species was also reported from plant litter, although these collections still may be mycoparasitic on saprobic species of Ascomycota decaying the plant material. Alternatively, it is possible that *H. blepharistoma* also is capable of decaying plant material.

Pycnopulvinus aurantiacus is a peculiar orange-coloured stilboid fungus growing on decaying palm leaf mid-ribs in the Neotropics (Toome & Aime 2014). Fructifications of this species are characterised by a basal cushion giving rise to a tubular neck up to 3 mm long, which apically bears a mucous droplet containing spores (**Fig. 5H**). Micromorphologically, *P. aurantiacus* is characterised by multiseptate spores and unclamped hyphae. Unfortunately, neither sporogenous cells nor spore germination have been observed and the spores were tentatively interpreted as asexual. As such, the lifecycle of *P. aurantiacus* remains unclear. This species has not been investigated for its septal pore apparatus or the presence of colacosomes. However, the authors proposed a possible mycoparasitic strategy for this fungus. During isolation attempts of *P. aurantiacus*, the authors obtained several isolates of the ascomycete *Ceratocystis paradoxa*, which was suggested as a possible host species. Although from molecular phylogenetic reconstructions *P. aurantiacus* has been recognised as the closest currently known relative of *Hyalopycnis blepharistoma*, a detailed comparison of sexual structures and ultrastructural characters remains to be done. Future attempts to cultivate *Pycnopulvinus* species may allow more detailed investigation of the sporogenesis and ultrastructure, and the discovery of a sexual state, if present.

Microbotryomycetes *incertae sedis*

Atractocolax pulvinatus is a colacosome-interacting species found in bark beetle galleries of decaying *Picea abies* and *Pinus sylvestris* logs (Kirschner & Oberwinkler 1999). This species produces pulvinate, gelatinous basidiomes and is characterised by transversally three-septate basidia producing statismospores and the presence of clamped hyphae. Basidiospores germinate by budding off yeast cells. A conidial stage has not

been observed. Ultrastructural observations based on a pure culture revealed the presence of colacosomes interacting with hyphae of its own mycelium, a phenomenon interpreted as self-parasitism (Kirschner & Oberwinkler 1999, Oberwinkler & Bauer 2018). Although no host species is known, a mycoparasitic strategy for *A. pulvinatus* has been suggested based on the presence of colacosomes (Kirschner & Oberwinkler 1999). The placement in Microbotryomycetes was tentative for a long time, based on the presence of colacosomes and septal pore ultrastructure. Schoutteten et al. (2023) provided DNA sequence data for this species and showed that it is a member of Microbotryomycetes based on molecular phylogenetic reconstruction.

The genus **Colacogloea** was established to accommodate *Platygloea effusa* (syn. *P. peniophorae*), an intrahymenial colacosome-interacting mycoparasite of *Peniophorella praetermissa* with a dimorphic lifecycle (Oberwinkler et al. 1991). Young stages of *C. effusa* produce yellowish slimy patches on the basidiome of its host, by which the mycoparasite can easily be detected macroscopically (**Fig. 5A**). In older stages, the white-coloured basidiome of the host disappears and minute yellowish-brownish tuberculate basidiomes of the mycoparasite remain, in which only some host remnants can be detected microscopically. Micromorphologically, the species is characterised by transversally three-septate basidia producing ballistospores, the absence of distinct probasidia, the presence of conidiophores producing thick-walled conidia, and the presence of hyphidia and clamped hyphae. Schoutteten et al. (2023) showed that *C. effusa* comprises a species complex, with at least six species in Europe which are associated with *P. praetermissa* and *P. pubera*. At least two distinct types of colacosome arrangement are known from this genus, i.e., colacosomes are arranged along touching hyphae of host and parasite, or in parasite-formed gall-like cells that surround host hyphae (**Fig. 5B**; Schoutteten et al. 2023).

Platygloea bispora is an intrahymenial mycoparasite of *Tubulicrinis* species and was recombined in the genus *Colacogloea* based on the presence of colacosomes (Oberwinkler & Bauer 1999). The colacosome interaction of this species is characterised by the formation of galloid cells by the parasite, which are invaginated by outgrows of host hyphae (Oberwinkler & Bauer 1999). Along the intrusion contact surface, colacosomes are formed densely, often visible as botryose structures by light and phase contrast microscopy. **Colacogloea allantospora** is an intrahymenial mycoparasite of *Tubulicrinis calothrix* (Bandoni et al. 2002). *C. allantospora* has not been investigated for its ultrastructure, but colacosomes have been observed by light microscopy (Bandoni et al. 2002). For both species, no cultures have been obtained, and DNA sequence data are not available. Consequently, their placement in Microbotryomycetes is tentative and only based on micromorphological similarities with other *Colacogloea* species. Kirschner & Oberwinkler (2001) described **Colacogloea papilionacea**, a colacosome-interacting mycoparasite isolated from bark beetle galleries of *Pinus sylvestris*. Peculiar characteristics of this species are the production of zygoconidia and spirally coiling hyphae around ascomycetous host hyphae, with formation of colacosomes at regular distances at the contact points (Bauer 2004). The host of *C. papilionacea* was identified as an ascomycetous fungus based on the ultrastructure of the cell wall and the presence of Woronin bodies near the hyphal septa.

Krieglsteinera lasiosphaeriae is a colacosome-interacting mycoparasite of *Lasiosphaeria ovina*. This species is macroscopically visible as thin hyaline stalks with apical slimy droplets growing on host perithecia (**Figs. 5C, 5D**; Pouzar 1987, Miller et al. 2003). This species has a unique micromorphology, with transversally three-septate basidia growing on large, clamped basidiophores. Each basidiophore gives rise to three basidia, each of which is subtended by a basal clamp connection. Basidia successively produce statismospores, accumulating in a slimy droplet at the top of each basidiophore. Basidiospores may germinate by budding yeast-like cells (Oberwinkler 2017), but no cultures have been obtained from this species. In some collections of *K. lasiosphaeriae*, a conidial phase is present, characterised by regularly branched conidiophores producing basally clamped conidia (Miller et al. 2003). Colacosomes are organised in galloid cells formed by the mycoparasite (**Fig. 5E**; Bauer 2004). No DNA sequence data are available for this species, and its placement in Microbotryomycetes is tentative and based on ultrastructural similarities only (Schoutteten et al. 2023).

Slooffia micra is a colacosome-interacting intrahymenial mycoparasite of *Myxarium podlachicum*. Initially described as *Platygloea micra*, Bourdot & Galzin (1924) did not recognise the presence of a host fungus. Based on morphological comparison, Hauerslev (1993) introduced *Achroomyces insignis* for a mycoparasite

of *M. podlachicum*, but did not detect the presence of colacosomes. Schoutteten et al. (2023) investigated the holotypes of both taxa and concluded that they are conspecific. Additionally, colacosomes were detected using epifluorescence microscopy and were organised in hyphae of the parasite that coil around host hyphae (Schoutteten et al. 2023). It is likely that *Cystobasidium sebaceum*, a colacosome-interacting mycoparasite of *Myxarium* sp., is also a member of the genus *Slooffia*.
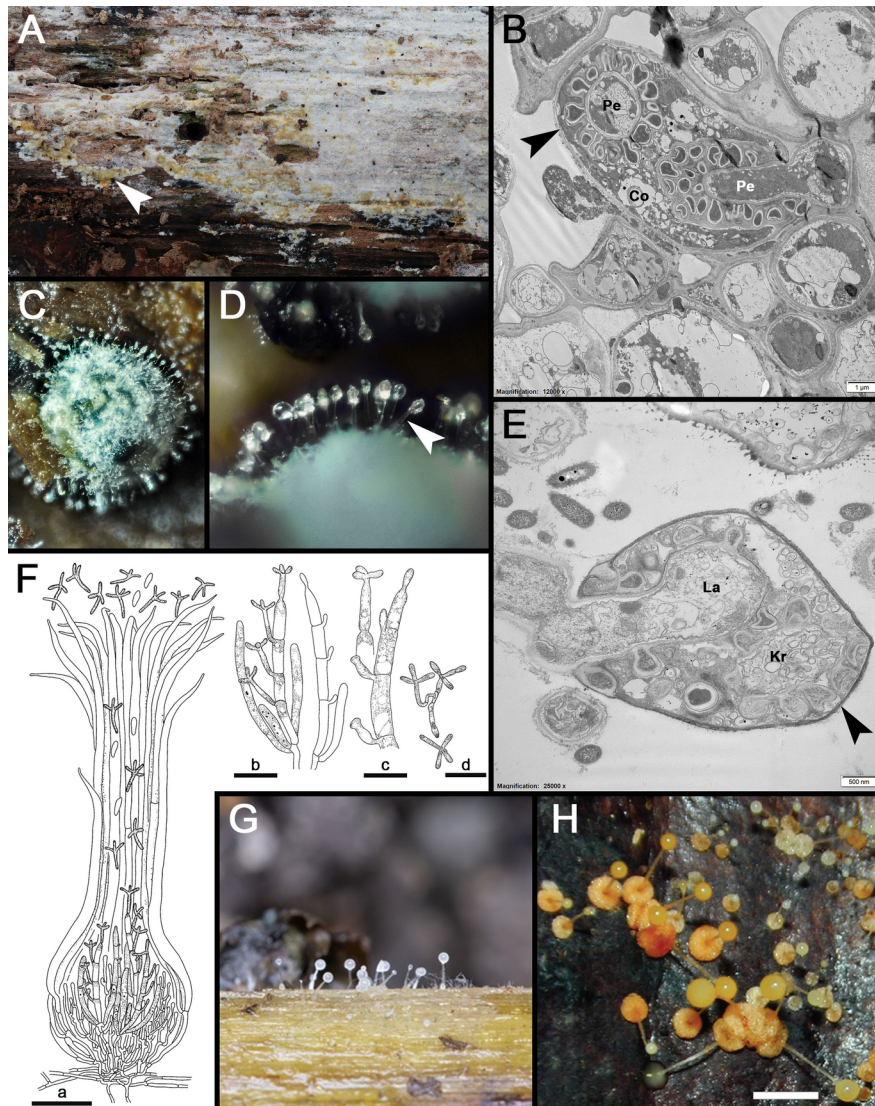
Figure 5: **Fig. 5. Mycoparasites in Microbotryomycetes. A.** Basidiome of *Peniophorella praetermissa*, infected with *Colacogloea universitatis-gandavensis*, visible as yellow patches (arrowhead) (specimen NS 21-013). © Nathan Schoutteten. **B.** Host-parasite interface of *P. praetermissa* and *Colacogloea,* showing an enlarged hyphal cell (arrowhead) of the mycoparasite (Co) which is invaginated by two host hyphae (Pe). Colacosomes surround the invaginating hyphae (specimen NS 20-022). © Nathan Schoutteten. **C–D.** *Krieglsteinera lasiosphaeriae* growing on ascomata of *Lasiosphaeria ovina. K. lasiosphaeriae* produces stilboid structures (arrowhead) consisting of a basidiophore which apically produces three basidia. These basidia successively produce basidiospores which are accumulated in a slimy droplet. © Jens H. Petersen. **E.** Host-parasite interface of *Lasiosphaeria ovina* and *K. lasiosphaeriae* (specimen GVA 20-002), showing a gall-like hyphal cell (arrowhead) of the mycoparasite (Kr) which is invaginated by two host hyphae (La). Colacosomes surround the invaginating hyphae. © Nathan Schoutteten. **F.** a: Pycnidioid basidiome and micromorphology of *Hyalopycnis blepharistoma*, showing tetraradiate basidiospores, oval conidia, and transversally septate basidia; b, c: detail, showing basidioles and septated basidia producing tetraradiate basidiospores; d: germinating basidiospores. Redrawn and modified from Oberwinkler et al. (1990). © Maoqiang He. Scale bars a = 40 μm; b, d = 20 μm, c = 10 μm. **G.** Pycnidioid basidiomes of *Hyalopycnis blepharistoma.* © Thorben Hülsewig. **H.** Stilboid fructifications of *Pycnopulvinus aurantiacus.* Reproduced with permission from Toome & Aime (2014). Scale bar = 2mm.

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4.6 Pucciniomycotina - Pucciniomycetes

With more than 8650 species described, Pucciniomycetes are by far the most speciose class in Pucciniomycotina (Begerow et al. 2018, He et al. 2019). Most species (> 8000) belong to the well-studied phytoparasitic order Pucciniales, comprising the rust fungi. The other species in this class are distributed over Helicobasidiales, Pachnocybales, Platygloeales, and Septobasidiales, of which only the Helicobasidiales are confirmed to contain mycoparasites.

Helicobasidiales

Mycoparasitism in Pucciniomycetes is restricted to members of the Helicobasidiales, more specifically to the haploid stages of *Helicobasidium* species (**Fig. 6B**). The *Helicobasidium* stages (i.e., the sexual, dikaryotic stage of the lifecycle) are phytopathogens with a broad host spectrum, that cause severe violet root rot in a multitude of plant host species (**Fig. 6C**). On the other hand, the *Tuberculina* stages of Helicobasidiales (i.e., the asexual, haploid stage of the lifecycle) are mycoparasites of phytoparasitic rust species (Pucciniales) (Lutz et al. 2004a,b). These **mycoparasitic haploid stages have long time been interpreted as distinct, anamorphic species** and were originally classified in the genus ***Tuberculina*** Tode ex Sacc. (Lutz et al. 2004a, Lutz et al. 2004b). *Tuberculina* stages specifically infect the aecia (i.e., haploid, dikaryotic fructifications) of rust species, on which they develop subepidermal pulvinate sporodochia (**Fig. 6A**). These structures consist of palisade-like arranged conidiophores, each of which gives rise to a single conidium (Aghayeva et al. 2016). The basidiomycetous nature of *Tuberculina* stages has been revealed by Lutz et al. (2004a) through molecular phylogenetic analyses. Traditionally, three *Tuberculina* species have been reported associated with aecia of more than 150 rust species (Lutz et al. 2004c). Many more names are available for *Tuberculina* species and there is a serious need for a taxonomic revision of the genus. Aime et al. (2018) called for protection of the name *Helicobasidium*, which is a widely used later synonym of the name *Tuberculina*.

The host-parasite interaction is characterised by a unique cellular interaction type: the **μμ-φυσιον πορε ιντεραςτιον** (Lutz et al. 2004a, Bauer 2004, Bauer et al. 2004). Based on TEM observations, the following hypothesis was proposed. **Cellular interaction between mycoparasite and host hyphae mainly takes place at the base of rust aecia in the plant tissue.** At the contact area, hyphal outgrows formed by the mycoparasite invaginate neighbouring host hyphae. Subsequently, the cell walls of both host and mycoparasite dissolve, and a **φυσιον πορε οφ 0.5−1 μμ διαμ.** is formed (**Fig. 6D**). The membrane of the micropore is continuous with the plasma membranes of the host and mycoparasite, establishing direct cytoplasmic contact between both interaction partners. Horizontal transfer of nuclei (**Fig. 6D**) and mitochondria from mycoparasite to host cells through these micropores has been observed by Bauer et al. (2004). After transfer to the host cell, **nuclei of the parasite migrate to the direct neighbourhood of host nuclei**, which indicates a possible interaction between nuclei of both species. However, no further research has been undertaken to investigate the molecular background of this parasitic interaction.

Infection of rust species with *Tuberculina* stages often results in a decreased growth of the phytoparasitic rust, whereas the mycoparasite starts to develop asexual sporodochia-like reproductive structures. Lutz et al. (2004c) performed in-situ infection experiments using different collections and cultures of *Helicobasidium*- and *Tuberculina* stages and inoculated a plethora of host genera. Phylogenetic analyses integrating morphological and ecological data revealed at least six monophyletic lineages, which were generally characterised by host specificity (at different levels) of the mycoparasitic *Tuberculina* stage (Lutz et al. 2004c). As stated by Lutz et al. (2004c), the host specificity of the *Tuberculina* stages is in sharp contrast to the apparently unspecific phytoparasitic *Helicobasidium* stages. However, it should be noted that integrative phylogenetic studies on this group are lacking, and the currently used species concept is still morphology-based (Roberts 1999, Uetake et al. 2002). This leaves room for undetected genetic diversity and host specificity in the phytoparasitic stages. Only in three out of six phylogenetic lineages, a clear link has been observed between *Helicobasidium* and *Tuberculina* morphs. One clade revealed a link between a *Helicobasidium purpureum* morph and a *Tuberculina persicina* morph. Two other clades linked a *Helicobasidium longisporum* morph

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with a *Tuberculina persicina* morph. For *T. maxima* and *T. sbrozzii*, no *Helicobasidium* -morphs have been found. This may either imply that these stages have not been discovered yet, or *T. maxima* and *T. sbrozzii* have lost the ability of sexual reproduction and the accompanying *Helicobasidium* stage.

Platygloeales

The order Platygloeales is based on the genus *Platygloea* J. Schröt. (syn. *Achroomyces* Bonord.), which is typified by the saprobic species *Platygloea disciformis* (Fr.) Neuhoff. This species produces greyish, cushion-like basidiomes on *Tilia* branches and is characterised by transversally three-septate basidia (Oberwinkler et al. 1990, Bruggeman-Nannenga 2011). Other taxa in this order comprise phytoparasites of Bryophyta, Pteridophyta, or Spermatophyta, also characterised by transversally septate basidia (Oberwinkler & Bandoni 1984). As can be seen in **Table 1**, many mycoparasites are listed in this order, although they most likely belong to other groups. Basidiomycetous mycoparasites in general display only a limited set of morphological characters, and many were tentatively assigned to the genera *Achroomyces* and *Platygloea* solely based on the presence of transversally septate basidia. Bandoni (1956) was one of the first to recognise the heterogeneity of this genus and stressed that most taxa probably belong to other genera. Many mycoparasites still reside in this class based on superficial micromorphological similarities, and correct classification of these taxa requires recollecting, cultivation, and generation of relevant types of data, especially DNA sequence data. A remarkable observation is that all of the currently sequenced mycoparasites that originally were classified in Platygloeales have been found to belong to other classes of Basidiomycota. It is likely that all mycoparasites still classified in Platygloeales belong to other groups, and mycoparasitism might not be prevalent in this order.
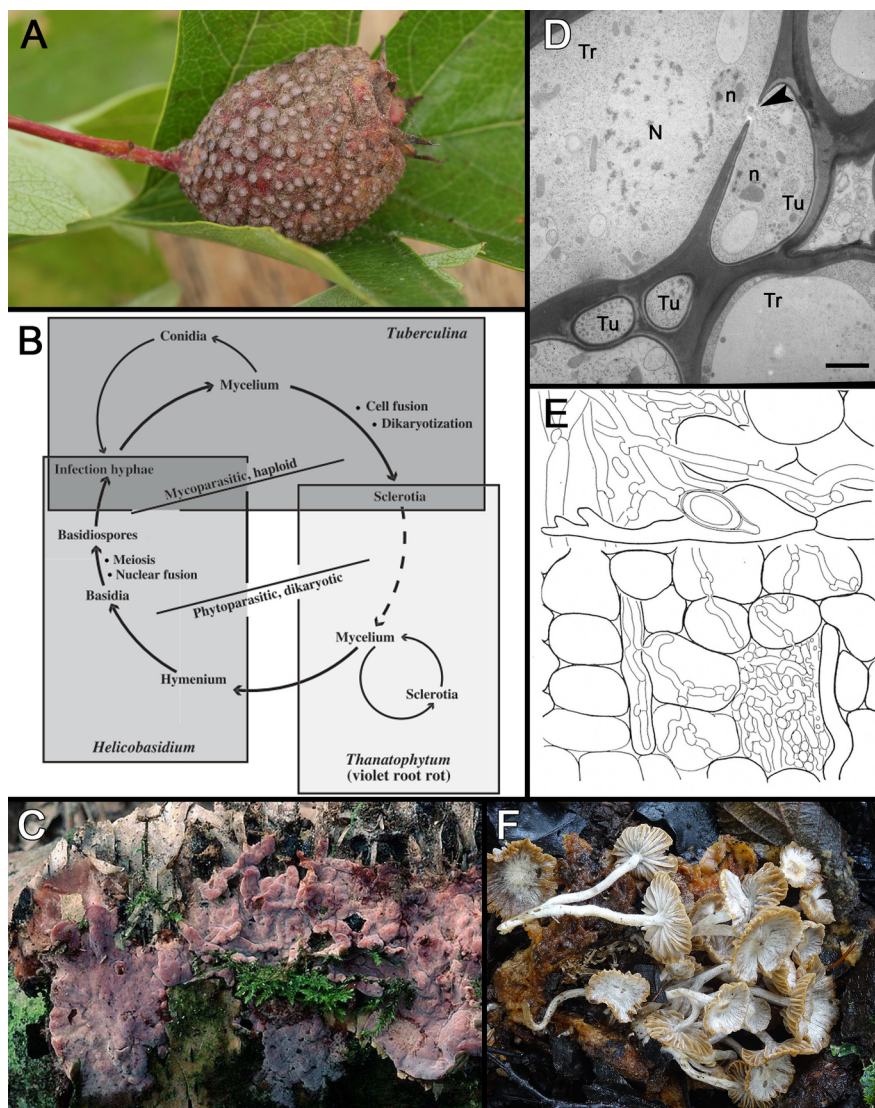
Figure 6: **Fig. 6. Mycoparasites in Pucciniomycetes (A–D) and Agaricomycetes (E–F). A.** Sporodochia-like structures of the haploid, mycoparasitic stage of *Helicobasidium purpureum*, infecting a rust; © Ole Martin. **B.** Lifecycle of *Helicobasidium* species, continuous lines represent experimentally proven links, dashed lines represent hypothetical links; reproduced with permission from Lutz et al. (2004b). **C.** Basidiome of the dikaryotic stage of *Helicobasidium purpureum*; ©Jens H. Petersen. **D.** Host-parasite interface of the haploid stage of *Helicobasidium purpureum* [as *Tuberculina persicina*] (Tu) and its host *Tranzschelia pruni-spinosae* (Tr), characterised by a micrometer fusion pore (arrowhead). Note that the nucleus of the host (N) is larger than the two nuclei of the mycoparasite (n) and that one nucleus of the mycoparasite is located in the host cell close to the nucleus of the host. **E.** Inter- and intracellular hyphae with clamps and one chlamydospore of *Asterophora parasitica* growing in and between hyphae of the host fungus; original drawing by Franz Oberwinkler. **F.** Basidiomes of *A. parasitica* growing on decaying basidiome of *Lactarius* sp.; © Roeland Enzlin.

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4.7 Pucciniomycotina - Spiculogloeomycetes

Spiculogloeomycetes is a rather small class comprising dimorphic *Spiculogloea* mycoparasites and taxa only known from yeast morphs (i.e., *Meniscomyces* spp. and *Phyllozyma* spp.) (Begerow et al. 2018, Wang et al. 2015a,b, Cao et al. 2021, Li et al. 2020). This clade was first recognised by Weiß et al. (2004) based on LSU and SSU rDNA sequences derived from two specimens identified as '*Mycogloea* sp. FO 40962' and '*Spiculogloea* sp. RB 1040'. The authors mentioned a host-parasite interaction via nm-fusion pore haustorial cells for both species, however, no other relevant ecological or morphological data was provided, and the exact identity of the mycoparasites and host species remained unclear (Weiß et al. 2004, Bauer et al. 2006). The anamorphic yeasts in this class have been isolated from phylloplanes of various plant species and belong to the genera *Phyllozyma* and *Meniscomyces* (Wang et al. 2015b, Li et al. 2020). Oberwinkler (2017) argued that these phylloplane yeasts may be asexual morphs of (yet unknown) mycoparasites and suggested that the yeast ballistoconidia may be a useful dispersal mechanism to reach a compatible host. Currently, five filamentous mycoparasites are known in the genus *Spiculogloea*, which all are growing intrahymenially in host basidiomes of corticioid fungi (**Fig. 7A, 7D**). A peculiar feature is the **ornamented, transversally three-septate basidia**, based on which these species have been assigned to the genus *Spiculogloea*. The genus name refers to this fine ornamentation on the basidia, originally designated as fine 'spicules' (**Fig. 7D**) (Roberts 1996). In some species, a distinct probasidium and/or a conidial stage were observed. A yeast morph was obtained from a *Spiculogloea* cf. *occulta* parasiting *Lyomyces sambuci* by Langer and Oberwinkler (1998) (**Fig. 7B**), and it can be expected that the other *Spiculogloea* species are dimorphic as well. Weiß et al. (2004) and Bauer et al. (2006) showed the **nm-fusion pore interaction enabled by haustorial cells** of *Spiculogloea* cf. *subminuta* [wrongly indicated as *Spiculogloea minuta*] with its host *Botryobasidium subcoronatum*. These haustorial cells are subtended by a clamp connection and are characterised by a widened base, giving rise to a short outgrow with a globular apex (**Fig. 7C, 7E**). A nm-fusion pore is formed at the contact surface of the haustorial apex and the host hypha, establishing cytoplasmic contact (**Fig. 7F**). Haustorial cells of *S. subminuta* were found to be dikaryotic (**Fig. 7E**; Bauer et al. 2006). DNA sequence data are available for none of the currently described *Spiculogloea* species, except for specimen '*Spiculogloea* sp. RB 1040' used in Weiß et al. (2004) and Bauer et al. (2006). Consequently, the placement of these species in Spiculogloeomycetes is tentative and it remains to be proven whether all species are congeneric. Also, the assessment of species boundaries and host specificity of these mycoparasites remains to be investigated.
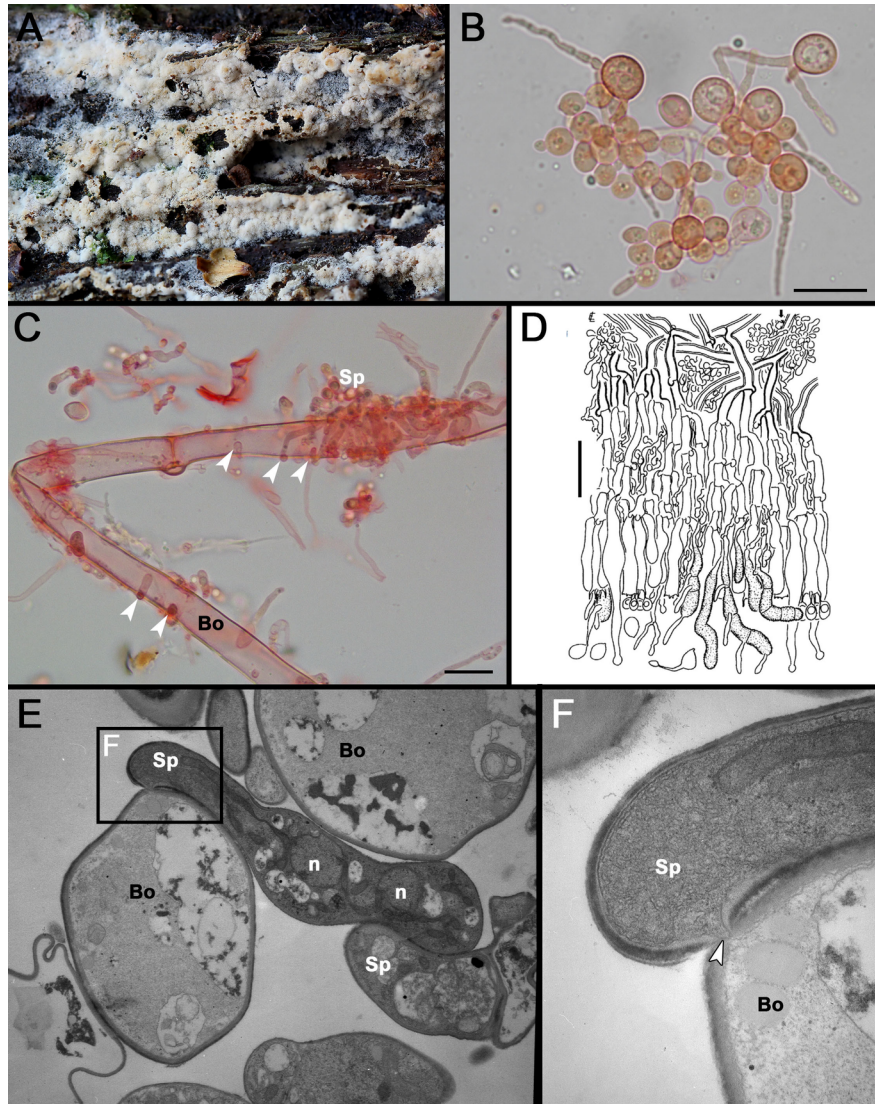
Figure 7: **Fig. 7. Mycoparasites in Spiculogloeomycetes. A.** Basidiome of *Botryobasidium subcoronatum* infected with *Spiculogloea subminuta*. Heavily infected specimens often display small gelatinous thickenings and slightly discoloured patches on the host basidiome; © Thomas Rödel. **B.** Basidiospores of *Spiculogloea occulta* in pure culture, germinating by hyphae and yeast cells; © Nathan Schoutteten. Scale bar = 10 μm. **C.** Hyphae and haustorial cells (arrowheads) of *S. subminuta* (Sp) coiling around a hypha of the host *Botryobasidium subcoronatum* (Bo) (specimen NS 19-420); © Nathan Schoutteten. Scale bar = 10 μm. **D.** Microscopic structures of *S. occulta* and its host *Lyomyces sambuci* (specimen GEL 607), note the ornamented basidia which are characteristic of the genus; reproduced with permission from Langer & Oberwinkler (1998). **E–F.** TEM of the host-parasite interface of *S. subminuta* (Sp) and *B. subcoronatum* (Bo) (specimen FO 38413). **E.** Haustorial cell of *S. subminuta* attaching to a hypha of the host *B. subcoronatum*. Note that the haustorial cell is dikaryotic (n). **F.** Detail of the haustorial apex where a nm-fusion pore is formed (arrowhead).

4.8 Pucciniomycotina - Tritirachiomycetes

Tritirachiomycetes is a small class of fungi that were formerly classified in Pezizomycotina, based on morphological similarities of the verticillate-branched conidiophores occurring in various ascomycetous genera. The first comprehensive phylogenetic and ultrastructural study of the genus *Tritirachium* was performed by Schell et al. (2011), which revealed the basidiomycetous nature of this group. At the ultrastructural level, Tritirachiomycetes are characterised by simple septal pores, which in at least two *Tritirachium* species are occluded by a structure resembling the *cystosome* found in Cystobasidiomycetes (see above). All species in this class reproduce asexually, and sexual reproduction has only been observed in *Paratritirachium curvibasidium* H.D.T. Nguyen, Tanney, N.L. Nickerson & Seifert (Nguyen et al. 2014). Members of Tritirachiomycetes have been isolated from various substrates (e.g., decaying plant remnants, insects, and human cornea and skin) and environments (e.g., indoor, outdoor and marine) from different regions in the world. At least one or two *Tritirachium* species (*T. dependens* and *T. egenum*; interpreted as synonyms by Schell et al. 2011) have been reported in association with *Penicillium* species (Limber 1940, Beguin 2010). *T. egenum* is unable to grow on traditional media without the presence of a *Penicillium rugulosum* strain or the addition of certain growth factors (Beguin 2010). Since no direct cellular interaction structures have been observed and no effect on the host species has been reported, this relationship was originally not designated as mycoparasitism. Instead, Beguin (2010) indicated the association of *T. egenum* and the accompanying *P. rugulosum* strain as a 'biotrophic mycosymbiosis'. However, some authors leave some room for interpretation by referring to this interaction as potential obligate mycoparasitism (Aime et al. 2014, Begerow et al. 2018).

4.9 Ustilaginomycotina - Ustilaginomycetes

Mycoparasitism remains largely unknown in Ustilaginomycotina, a group dominated by phytoparasites and animal-associated yeasts. Only recently, *Quasiramularia phakopsoricola* was described as a mycoparasite of the rust *Phakopsora ampelopsidis* (Pucciniales) (Kolařík et al. 2021). *Quasiramularia phakopsoricola* is known to reproduce asexually only, and morphologically this species displays more similarities to other mycoparasites from the genus *Ramularia* (Ascomycota) than to other members of Basidiomycota. Interestingly, ITS sequences of this species are characterised by low GC content compared to other members of Ustilaginomycotina, and BLAST searches render no significant results. Phylogenetic reconstructions incorporating LSU, SSU, and RPB2 DNA sequence data showed *Q. phakopsoricola* to be placed on a long branch within Ustilaginomycetes, prompting the authors to propose the monotypic order Quasiramulariales. It is possible that more diversity remains to be discovered in this clade. Unfortunately, no details on the host-parasite interface are available, and the interaction mechanism remains unknown.

A few yeasts in Ustilaginomycotina have been reported to have antagonistic interactions with other fungi, enabled by the production of antibiotic substances. *Anthracocystis flocculosa* (Traquair, L.A. Shaw & Jarvis) M. Lutz & Piatek (syn. *Pseudozyma flocculosa*) was repeatedly isolated from leaves infected with powdery mildews, and is used as a biocontrol agent against these phytoparasites. This fungus was shown to produce flocculosin, a glycolipid with antifungal activity against a variety of fungi (Mimee et al. 2005). Other species producing antibiotic glycolipids and modified long-chain fatty acids are *Golubevia pallescens* (Gokhale) Q.M. Wang et al., and *Robbauera albescens* (Gokhale) Boekhout et al. (Begerow et al. 2014, 2017). However, it is unclear whether these species are able to derive nutrients from other fungi in natural conditions. Also, no host-parasite interaction structures were reported for these species so far. Consequently, these species should be viewed as fungal antagonists, and a real mycoparasitic nature of these species remains to be proven.

4.10 Agaricomycotina - Tremellomycetes

Tremellomycetes is the earliest diverging group within Agaricomycotina, and the most speciose group of mycoparasites in Basidiomycota. This class comprises a heterogeneous group of fungi, which is reflected in

their ecology, morphology, and lifecycles. The two major ecological groups in Tremellomycetes are parasites of non-lichenized fungi on the one hand, and lichen parasites on the other hand. Both groups display a large diversity in basidiome morphology, reproductive structures, and host species diversity (Millanes et al. 2011, Weiß et al. 2014, Diederich et al. 2022). A relatively small number of species of Tremellomycetes distributed over Tremellales and Trichosporonales engage in zooparasitic and zoopathogenic interactions. These lineages comprise the causal agents of severe diseases such as cryptococcosis (*Cryptococcus* spp.), Onychomycosis and Trichosporonosis (*Trichosporon* spp.). These fungi are lethal opportunistic human-associated pathogens that mainly manifest in immunocompromised individuals, and cause over 600.000 new infections and a similar number of deaths annually (Kwon-Chung et al. 2014, Hagen et al. 2015, de Almeida Júnior & Hennequin 2016, Begerow et al. 2017, Passer et al. 2019, Li et al. 2020b). A fourth group comprises a considerable number of species only known from yeast morphs, isolated from a wide range of habitats and various substrates. Most of these yeasts were assigned to this class based on molecular phylogenetic analyses and some physiological characteristics, but their ecological roles remain yet to be determined (Sampaio & Fonseca 1995, Liu et al. 2015, Li et al. 2020).

The majority of **basidiome-forming Tremellomycetes can be considered as mycoparasites**. Basidiomes of Tremellomycetes are highly diverse and range from hyaline inconspicuous pustules to colourful fleshy cerebriform or foliate structures formed by hyphae embedded in a gelatinous matrix (**Figs. 8A–F**). Various species of Tremellomycetes develop basidiomes on tree branches, at some distance from the basidiomes of their host fungus. An illustrative example is *Phaeotremella frondosa*, which often co-occurs with a *Stereum* species on the same branch (**Fig. 8D**). Since the *Tremella* and *Stereum* basidiomes are not necessarily developing close or adjacent to each other, the mycoparasitic nature of these species is not always obvious. In many cases, the host-parasite interaction occurs along the mycelium, hidden in the substrate. Because of this, many species described in the nineteenth and twentieth centuries were originally regarded as saprobes, and little is known about their substrates and co-occurring species which are potential hosts. Some tremellomycetous mycoparasites do not develop own basidiomes, but grow **intrahymenially** in their host species (**Fig. 8G**), e.g., species of *Filobasidiella*, *Heteromycophaga*, *Phragmoxenidium*, *Piskurozyma*, *Syzygospora*, *Tremella*, and *Xenolachne* (**Table 1**).

Mycoparasites in Tremellomycetes belong to Filobasidiales, Holtermanniales, Tremellales, or Trichosporonales. However, a considerable amount of currently described tremellomycetous mycoparasites is not yet characterised by DNA sequence data. Consequently, they cannot be assigned with certainty to the existing clades and we listed them as Tremellomycetes *incertae sedis* in **Table 1**. This implies that mycoparasitism may occur in more clades than currently known. We expect that many teleomorph-anamorph links remain to be discovered. The yeast morphs of various mycoparasites may be already known and described as separate genera and species. Most tremellomycetous mycoparasites are dimorphic, although for many species neither living yeast cultures nor DNA sequence data are currently available, impeding systematics of the class. A notable exception to dimorphism seems to be species of *Xenolachne*, which are characterised by statismosporic basidia (Bandoni 1995). In several cultivation experiments, basidiospores failed to germinate (Schoutteten & Miettinen, pers. obs.). However, it may be possible that the initiation of the haploid yeast morph requires special conditions.

To date, all tremellomycetous mycoparasites that were investigated for their host-parasite interface using TEM were found to **engage in nm-fusion pore interaction enabled by haustorial cells**. Some early studies investigated the ultrastructure of the host-parasite interface of various tremellomycetous mycoparasites, but failed to find or recognise the typical nm-fusion pores (Bezerra & Kimbrough 1978, Oberwinkler & Bandoni 1981, 1982). Bauer & Oberwinkler (1990) for the first time reported that in haustorial cells of *Tetragoniomyces uliginosus* (Trichosporonales), a small membrane-bound channel of approx. 14–19 nm diameter was formed, establishing a cytoplasmic bridge with a hyphal cell of its *Rhizoctonia* host fungus. Later, similar nm-fusion pores were confirmed based on TEM in haustorial cells of the following Tremellomycetes: *Phragmoxenidium mycophilum*, *Tremella giraffa*, *T. mesenterica*, *T. occultifuroidea*, and *Trimorphomyces papilionaceus* (Oberwinkler et al. 1990, Chen 1998, Chen et al. 1999, Bauer 2004). We hypothesise that the majority of mycoparasites with tremelloid haustorial cells in Tremellomycetes and Pucciniomycotina inter-

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act with their hosts via such nm-fusion pores, but some variation in specific species may occur, such as in *Naohidea sebacea* (see Cystobasidiomycetes). One variation on the nm-fusion pore interaction in Tremellomycetes was reported from **Syzygospora pallida** (Filobasidiales) and its host *Phanerochaete cremea* (Bauer & Oberwinkler 1990b). *S. pallida* develops haustorial cells, of which the haustorial apex partly invaginates a host hypha instead of attaching to the surface. Along the contact surface, the cell wall of the host partly dissolves, and multiple membrane-bound nm-fusion pores are formed, connecting the mycoparasite and host cytoplasms.

The genus **Cryptococcus** (Tremellales) is a noteworthy group of (dimorphic) fungi of which the filamentous morphs are morphologically similar between the species, but the ecology of the species differs remarkably. The filamentous morph is characterised by typical basidia, which are stalked, apically swollen and partially longitudinally septate, and usually produce four basidiospores. Basidiospores are formed in a successive manner, and individual chains of up to 40 basidiospores can develop. Interestingly, the basidial stage of several Cryptococcus species can be obtained on V8 medium. The *Cryptococcus neoformans* and *C. gattii* species complexes comprise opportunistic human-associated pathogens, of which the yeast morphs cause lethal infections mainly in immunocompromised patients (Kwon-Chung 2014, Hagen et al. 2015, Passer et al. 2019). Yeast morphs of these species are characterised by an extracellular antigenic polysaccharide capsule. Hagen et al. (2015) formally recognised seven species in this group, which were discriminated using several methodologies such as multilocus phylogenetic reconstructions and MALDI-TOF MS, and found that the species differ in pathogenicity, physiological aspects, and susceptibility to antifungal compounds. Interestingly, haustorial cells were reported from the filamentous morph of *Cryptococcus neoformans* (Kwon-Chung 1976, 2011, Oberwinkler et al. 1982, Bandoni 1995), but it is unclear if haustorial branches can be developed by all species in this human-pathogenic lineage. As suggested by Bandoni (1995), the presence of haustorial cells in the filamentous morph of this species may indicate at least mycoparasitic capabilities during part of its lifecycle. However, a mycoparasitic interaction between species of the *C. neoformans* lineage and a host fungus has never been reported. In the genus *Cryptococcus*, three closely related non-pathogenic saprobic yeast species are known, namely *C. amylolentus* (Van der Walt, D.B. Scott & Klift) Golubev, *C. floricola* Yurkov et al., and *C. wingfieldii* (Van der Walt, Y. Yamada & N.P. Ferreira) Yurkov et al. Passer et al. (2019) used performed genetic crossing experiments and genomic comparisons between isolates of these species to investigate species boundaries and genomic divergence. Filamentous morphs with basidial stages were observed in culture for *C. amylolentus* and *C. floricola*, and basidia are similar to those observed in the *C. neoformans* / *C. gattii* species complex. Haustorial branches have not been reported from species in this presumed saprobic lineage, but it cannot be ruled out that these species have mycoparasitic capabilities. A third lineage in the genus *Cryptococcus* represents *C. depauperatus*, of which only a filamentous morph with a basidial stage is known. This species was isolated from scale insects infected with the entomopathogenic fungus *Verticillum lecanii*. Ginns & Malloch (2003) showed that in co-culture, C. depauperatus develops haustorial cells that connect to hyphae of *V. lecanii*. As such, it may represent a mycoparasite specialised on an entomopathogenic fungus. A fourth lineage represents **Cryptococcus luteus**, which develops as a mycoparasite in the hymenium of its host, *Granulobasidium vellereum* (**Fig. 8G**; Roberts 1997a). The host-parasite interface is characterised by haustorial cells produced by *C. luteus*. Similar to *C. depauperatus*, this species is only known from the filamentous morph which is characterised by the typical basidia forming four chains of basidiospores. However, this species was not grown in culture, and its phylogenetic position and relation to the previously discussed species remains elusive. An interesting hypothesis is that all *Cryptococcus* species have mycoparasitic capabilities and that in the lineage of *C. neoformans* additional mechanisms evolved allowing opportunistic infections of humans. A pure culture and whole genome sequencing of *C. luteus* would provide possibilities for genomic comparison with the other known species in this genus.

An enigmatic group in the Tremellomycetes is comprised of the genus **Sirobasidium**. Species in this genus are characterised by pustulate to cerebriform basidiomes, develop typical two- or four-celled basidia in chains, and have a dimorphic lifecycle. Around ten species are described, but cultures and DNA sequence data are available for five species only (Rödel & Putzmann 2015, Yamada et al. 2022). Previous molecular phylogenetic reconstructions have shown that the genus is polyphyletic within the Tremellales (Liu et al.

2015, Kachalkin et al. 2019, Yamada et al. 2022). The species included in **Table 1** have constantly been reported as growing in association with pyrenomycetous fungi, and hence can be regarded as fungicolous. Because of these associations, several authors suggested a possible mycoparasitic nature for these species, but **no haustorial cells or other host-parasite interaction structures have ever been reported** (Bandoni 1995, Bandoni et al. 2011, Yamada et al. 2022). If these species are true mycoparasites, the host-parasite interface might well be located deeper in the substrate, or another yet unknown type of interaction mechanism is involved. Yamada et al. (2022) stated that haustorial cells have been reported once, but these authors did not specify for which species. Unfortunately, we were not able to retrieve this report in literature.
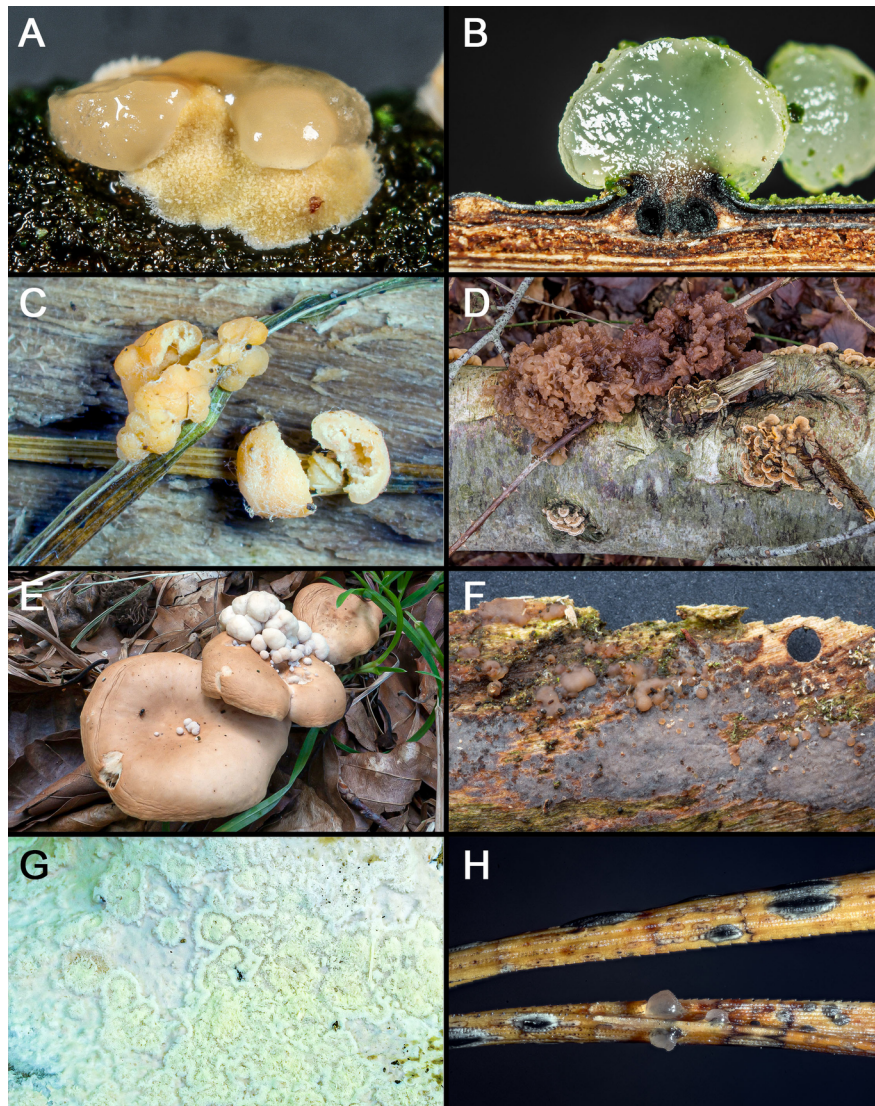
Figure 8: **Fig. 8. Mycoparasites in Tremellomycetes. A.** Pustulate basidiome of *Tremella simplex* growing on the basidiome of its host *Aleurodiscus disciformis*. **B.** *Tremella globispora* growing over ascomata of its host *Diaporthe* sp.**C.** Basidiome of *Tetragoniomyces uliginosus*. Note that the structures are hollow on the inside. **D.** Foliose basidiome of *Phaeotremella frondosa* growing on a branch near its host *Stereum* sp. **E.** Basidiomes of *Syzygospora tumefaciens* growing on the caps of its host *Gymnopus dryophilus*. **F.** Basidiome *Peniophora lycii* infected with*Tremella versicolor*, visible as orange pustules. **G.** Basidiome of *Granulobasidium vellereum*, infected with the intrahymenial mycoparasite *Filobasidiella lutea*, visible as a yellowish pruinose layer developing on the host. **H.** Pustulate basidiomes of *Sirotrema translucens* developing on ascomata of its host. Photos D and F © Roeland Enzlin, other photos © Jens H. Petersen.

4.11 Agaricomycotina - Agaricomycetes

Agaricomycetes, the group comprising the mushroom-forming fungi, are dominated by saprobic, mycorrhizal, or phytoparasitic fungi. **Rare transitions to mycoparasitism occurred in a few genera or**

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species in Agaricales and Boletales. Well-known examples include members of the genera *Asterophora*, *Buchwaldoboletus*, *Pseudoboletus*, and *Squamanita*, species of which are all considered to have at least partly mycoparasitic capabilities. Other examples comprise some species in genera which are dominated by species with other ecological strategies, such as representatives in the genera *Collybia*, *Dendrocollybia*, *Entoloma*, *Psathyrella*, *Rhodophana*, and *Volvariella*. Contrary to mycoparasites in Pucciniomycotina and Tremellomycetes, **little is known about host-parasite interaction mechanisms of mycoparasites in Agaricomycetes**. Fusion-pore interaction, colacosome interaction, or other specific interaction structures are not known in this group. Oberwinkler (2012) reported the presence of inter- and intracellular hyphae of *Asterophora* species in decaying or dead basidiomes of Russulaceae (**Fig. 6E, 6F**). Given the strongly decayed nature of the host, he pointed out that these species generally are regarded as saprobes rather than mycoparasites. Koch and Herr (2021) investigated the interaction between *Entoloma abortivum* and its host, *Armillaria* spp., at the transcriptome level. The interaction alters the development of host basidiomes, leading to the formation of structures indicated as carpophoroids. Caiafa and Smith (2022) proposed a dual trophic mode, including saprobic and mycoparasitic capabilities for *Buchwaldoboletus* species. By applying *in vitro* confrontation experiments with a variety of wood-decay fungi as hosts, the authors showed that hyphae of the mycoparasite coil around host hyphae. Similar *in vitro* confrontation experiments involving various basidiomycetous wood-decaying fungi indicated that some species show temporal necrotrophic mycoparasitism. These interactions likely play a role in competition for substrate colonisation and may be a temporary phase (Griffith & Barnett 1967, Rayner et al. 1986, Hiscox et al. 2018, Wieners et al. 2023). Most likely, after securing sufficient mycelial domain in the wood substrate, these fungi switch to a saprobic lifestyle. These examples illustrate that **mycoparasitism may often be a temporary phase during competition processes in lifecycles of fungi which have capabilities for multiple nutritional strategies** (Hiscox et al. 2018). However, such *in vitro* experiments should be interpreted carefully. Jeffries (1995) stated that even the unequivocal demonstration of a parasitic association between two species under laboratory conditions does not prove that such relationships between the respective species also occur in natural conditions.

5. Conclusions and general remarks

The trophic strategy of mycoparasitism in Basidiomycota is phylogenetically widely distributed, covering three subphyla and at least ten different classes: Agaricomycotina (Agaricomycetes, Tremellomycetes), Pucciniomycotina (Agaricostilbomycetes, Classiculomycetes, Cystobasidiomycetes, Cryptomycocolacomycetes, Microbotryomycetes, Pucciniomycetes, Spiculogloeomycetes), and Ustilaginomycotina (Ustilaginomycetes). For our compilation, we were able to identify at least 201 basidiomycetous mycoparasites. For the vast majority of them, no DNA sequence data or insights in host-parasite interaction mechanisms are available. Because of their often small dimensions and especially the hidden lifestyle of intrahymenial mycoparasites, we assume that many species have not yet been discovered, and the real diversity of mycoparasitic Basidiomycota is probably much higher than presently known. Given the heterogeneous phylogenetic relationships of these mycoparasites, they comprise an important group that cannot be neglected in attempts to infer the evolutionary relationships of Basidiomycota.

Current knowledge suggests that basidiomycetous mycoparasites have evolved two main types of host–parasite interaction mechanisms: fusion interaction and colacosome interaction. In fusion interaction, mycoparasites produce small membrane-bound channels that connect the cytoplasm of the host and parasite. Two distinct types of fusion interaction can be recognised based on the channel pore diameter: nanometer-fusion pores and micrometer-fusion pores. Nanometer-fusion pores are found in various classes in Pucciniomycotina and Tremellomycetes, while micrometer-fusion pores are exclusive to the class Pucciniomycetes. The exact function of these fusion pores has not been investigated yet, but they presumably facilitate nutrient transfer and potentially even transfer of nuclei in the case of micrometer-fusion pores. The colacosome interaction, on the other hand, is only known in a limited number of mycoparasites in Cryptomycocolacomycetes and Microbotryomycetes, and its precise mechanism remains unknown. No clear interaction structures have been

reported for mycoparasites in Agaricomycetes and Ustilaginomycetes, leaving the mechanism of nutrient transfer from host to parasite as an area requiring further investigation.

For many basidiomycetous mycoparasites, the mycoparasitic strategy represents only a temporal phase, and often alters with other trophic stages, depending on lifecycle transitions or environmental conditions. In mycoparasites with a dimorphic lifecycle, the mycoparasitic stage correlates with the dikaryotic stage in the filamentous morph, whereas the yeast morph generally represents the haploid stage with a saprobic ecology. In Helicobasidiales, on the contrary, the mycoparasitic phase correlates with the haploid stage, and is altered with a phytoparasitic dikaryotic stage. In several wood-decaying Agaricomycetes, mycoparasitism is a temporal phase linked with competition and depends on the presence of other fungal species in the same substrate. Taking this into account, only a few species can be considered as purely mycoparasitic, and many 'mycoparasites' have a broader range of capabilities to fulfil their nutritional requirements. Consequently, assigning fungal species to just one ecological category such as mycoparasitism is too simplistic.

6. Acknowledgements

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