Phylogeny, biogeography and host specificity of smut fungi

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Abstract: Smut fungi contain some of the most important and devastating plant parasites in agriculture. With the rise of molecular methods in the last 30 years, the understanding of evolution, ecology, genetics and molecular biology of this group of fungi has changed substantially. Additionally, the rise of high-throughput genomics and transcriptomics in recent years made an enormous impact and accelerated research. But not only methodological advances changed our understanding of the biology of smut fungi. An important conceptual recognition was the clustering of the many anamorphic lineages within the smut fungi. In this review we highlight some of the newer insights gained on smut fungi and concentrate on new developments in phylogenetics, the inclusion of anamorphic taxa, mechanisms of parasite-host interaction, biogeography, and host specificity. A focus thereby is the comparison of these topics in the two main lineages of smut fungi, Ustilaginomycotina and Microbotryales.

1. Introduction

The systematics of fungi has changed dramatically over the last three decades. Especially molecular phylogenetics and the increasing number of taxa included have regularly challenged traditional views of the evolution in this kingdom (Oberwinkler 1987, Hibbett et al. 2007, McLaughlin & Spatafora 2014, 2015). Closer scrutiny of groups consisting of only a handful of studied species have shown a high potential to contain overlooked, inconspicuous species (de Beer et al. 2006, Boekhout et al. 2003, 2006). Smut fungi have experienced several systematic rearrangements in the last 25 years, based on studies of morphology, ultrastructure and molecular phylogenetics. Their plant parasitic life-style has been the main reason for the analysis of these fungi, and early approaches to resolve phylogenetic relationships have focused on the structures relevant for plant parasitism. Molecular studies, however, have shown that smut fungal lineages are more diverse and may include several lineages that have never been associated with a smut syndrome (e.g. Begerow et al. 2014, Wang et al. 2015a, 2015b).

Most fundamental in the study of phylogenetic relationships of smut fungi has been the realization that the smut syndrome has evolved independently several times. Studies based on ultrastructure (Bauer et al. 1997), biochemistry (Prillinger et al. 1991) and molecular phylogenetics (Blanz & Gottschalk 1984, Begerow et al. 1997), determined that at least two smut fungal lineages evolved in the Basidiomycota (i.e. Microbotryales and Ustilaginomycotina). Even after the separation of Microbotryales from Ustilaginomycotina, the monophyly of Ustilaginomycotina, the largest smut fungal group, has been the topic of ongoing discussions. The separation of Entorrhizomycota has been

the second major step and resulted in good support for the monophyletic Ustilaginomycotina within Basidiomycota (Bauer et al. 2015).

Smut fungi have traditionally been characterized by plant-parasite interactions and even with the use of molecular tools, studies have not included species lacking a plant interaction into the system of smut fungi (Begerow et al. 1997, 2006, 2014, McTaggart et al. 2012). The incorporation of taxa not exhibiting the smut syndrome resulted in newly delimitated groups and sometimes questioned the traditional view of smut fungal evolution. The skin associated Malasseziales, for instance, was the first yeast lineage integrated into Ustilaginomycotina. Genomic data of this taxon support a lack of plant interaction as many genomic regions involved in plant interaction seem to have lost their function (Xu et al. 2007). Additional groups not showing a smut syndrome have been discussed within the Ustilaginomycotina, whereby the understanding of their respective ecological niches needs more detailed study. Molecular phylogenetics combined with studies on ecology, life history traits, species interactions, genetics and genomics will improve our biological understanding of smut fungi.

Besides the insight that not all lineages can be considered classical smut fungi, the smut syndrome and host-parasite interaction is still the main characteristic of most smut fungal taxa. Thus, host identity is still a prevalent characteristic for species identification (e.g. Piątek et al. 2012, 2013). The genetic basis of the smut syndrome, the infection mechanisms and interaction with the host are only partly understood and a focus of ongoing research (Kämper et al. 2006, Brefort et al. 2009, Perlin et al. 2015). The majority of smut fungi are known to infect only one or a few, often closely related plant species (Begerow et al. 2004) and co-speciation as a mechanism had a long explanatory tradition for the observed evolutionary patterns in this group. Other studies are trying to understand the genetic and molecular underpinnings of host specificity and mechanisms of parasite-host interaction.

This review will highlight recent studies concerning ecology, evolution, phylogeny and host specificity of smut fungi and will compare similarities and differences of Ustilaginomycotina and Microbotryales.

2. Phylogeny and evolutionary trends of smut fungi

There are almost 1900 smut fungal species known (Vánky 2012, Begerow et al. 2014, Aime et al. 2014). While the Microbotryales consist of about 120 species in 9 genera and two families, the Ustilaginomycotina harbour the majority of smut fungi. More than 75 % of recognized smut fungal species belong to the class Ustilaginomycetes. The members of this class are ultrastructurally characterized by enlarged plant-interaction zones, in contrast to Exobasidiomycetes with local interaction zones (Bauer et al. 1997, Begerow et al. 2014).

Fig. 1: Smut syndrom of different species of Ustilaginomycotina and Microbotryales
a) *Urocystis flocculosa* on *Helleborus foeditus* (Photo: Sascha Lotze-Engelhard), b) *Anthracoidea karii* on *Carex dioica* (Photo: Anja Feige), c) *Thecaphora oxalidis* on *Oxalis lanata*, petals removed (Photo: Francois Roets), d) *Microstroma alba* on *Quercus* sp. (Photo: Andrey Yurkov), e) *Exobasidium cassiopes* on *Cassiope tetragona*, f) *Laurobasidium lauri* on *Laurus nobilis*, g) *Microbotryum scabiosae* on *Knautia arvensis*, h) *Microbotryum saponariae* on *Saponaria officinalis*, i) *Entorrhiza casparyana* on *Juncus articulatus*.
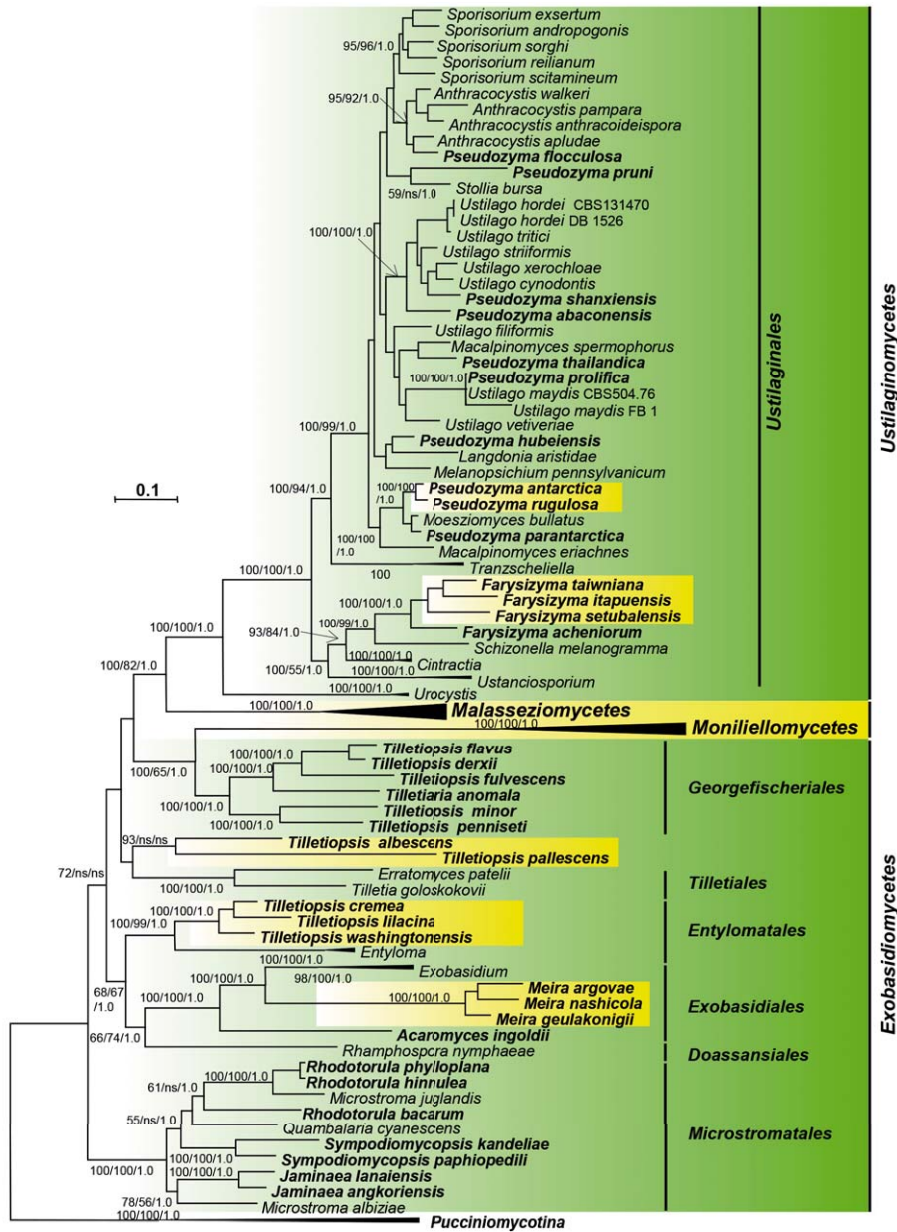
Fig. 2: Phylogenetic tree of Ustilaginomycotina based on a maximum likelihood analysis of sequences of SSU rRNA, partial LSU rRNA, ITS region (including 5.8 S rRNA), RPB1, RPB2, TEF1 and CYTB genes. Taxa in bold represent yeasts. Green lineages include mainly plant parasitic fungi, yellow lineages potentially are exclusively anamorphic, yeast or yeast-like fungi. Bayesian probabilities (PP) and bootstrap percentages (BP) from 1000 replicates of maximum likelihood and maximum parsimony analyses are shown respectively from left to right on the deep and major branches resolved. Branch lengths are scaled in terms of expected numbers of nucleotide substitution per site. Note.: ns, not supported (PP < 0.9 or BP < 50 %). Figure adapted from Wang et al. 2015a.

Species in the two new Ustilaginomycotina classes Malasseziomycetes and Moniliellomycetes (Wang et al. 2014) are only known in their anamorphic yeast phase and do not fit the morphological concept of the interaction zone presented by Bauer et al. (1997). The exclusion of the former member Entorrhizales as part of the Entorrhizomycota (Bauer et al. 2015) is based on a multigene phylogeny and seems to be appropriate given the overview of the known characters. It remains open, whether *Entorrhiza* and *Talbotiomyces* (Riess et al. 2015) should be considered classical smut fungi that parasitize their host or if their association results in another ecological outcome. At least their appearance in root nodules is different than a typical smut syndrome in flowers or leaves (Fig. 1). Thus, in the present description the Ustilaginomycotina are monophyletic and comprise four classes that are very diverse – not only in their genetic diversity, but also in morphological and ecological terms.

The aforementioned incorporation of anamorphic, cryptic, or inconspicuous species into phylogenetic analyses, additionally complicates the interpretation of evolutionary patterns in the smut fungi. For instance, Microstromatales and Georgefischeriales both consist of inconspicuous species recognized only by few experts in the field. Many species in these groups have been most probably overlooked. A much larger species diversity was therefore already predicted in earlier works (e.g. Begerow et al. 2000). Several studies in the last 15 years revealed an increasing number of isolates within the Ustilaginomycotina, and corroborated the previous assumption (Boekhout et al. 2003, 2006, Wang et al. 2015a). However, as these isolates were obtained as saprobic strains in cultures from the environment, their potential host or their parasitic nature is not known and these findings often resulted in even more questions. The discovery that the Moniliales, a group thought to belong to the Ascomycota, belongs to the Ustilaginomycotina was an additional breakthrough for a more complex phylogeny and systematics of parasitic lineages and yeast-like lineages in the Ustilaginomycotina (Wang et al. 2014).

Most smut fungi produce dark powdery, thick-walled teliospores that are produced on leaves, in flowers, anthers, inflorescences, on the stem, or parts of the roots (Fig. 1) of the plant host. Exceptions, such as members of the genus *Entyloma* produce hyaline instead of melanized spores within the plant tissue. Thick-walled teliospores are considered to be adaptations to survive harsh environments in order to germinate under favourable conditions. From our own experience we know that teliospores from herbarium specimens of some species of *Ustilago* are still viable after 10 years (unpublished data). In contrast, in some genera (e.g. *Anthracoidea*, *Cintractia*) newly formed teliospores germinate very badly and hibernation is often a precondition for germination (Kukkonen 1961). The sorus location and spore morphology of many species suggest an additional adaptation to the mode of their dispersal, which for species producing powdery teliospores is thought to be by wind. In some lineages, such as Georgefischeriales or Entylomatales in the Exobasidiomycetes (Bauer

et al. 2001, BEGEROW et al. 2002b), the teliospores are not released directly in the wind, but degradation of the leaves is required. Specific characteristics, such as spore balls with sterile cells in the Urocystales have been discussed as an adaptation to aquatic dispersal (BAUER et al. 1999), but experimental proof for such a claim is lacking so far. Strikingly, even pollinator distribution has evolved in several taxa, where the fungus sporulates in the anthers of the hosts. Based on available phylogenies it seems that anther smuts have evolved at least two times in the genus *Microbotryum* (KEMLER et al. 2006, 2009) and two times in the Urocystales, namely the genera *Antherospora* and *Thecaphora* (PIĄTEK et al. 2013, ROETS et al. 2012, VÁNKY & LUTZ 2007). Exobasidiales and Microstromatales have even reduced the teliospore and are distributed by basidiospores or sporidia only (BEGEROW et al. 2001, 2002a). It seems, these lineages on woody plants can survive without resting spores and teliospores are obsolete and therefore reduced in these two orders. However, as Tilletiales are still part of the Exobasidiomycetes, we assume that the characteristics of Ustilaginomycetes represent the ancestral form in terms of the described smut syndrome.

The convergent evolution of the smut life cycle that alternates between haploid, saprobic yeasts and dikaryotic, plant-parasitic hyphae is an astonishing fact. However, the dikaryotic hyphae is an ancestral characteristic common to all Dikarya, including Basidiomycota (JAMES et al. 2006, HIBBETT et al. 2007). Comparisons of life-cycles and the relevance of yeast stages in various lineages of heterobasidiomycetes suggest an origin of the yeast stage that pre-dates the origin of the Basidiomycota (OBERWINKLER 1985, 1987) and recent comparative genomic studies support an ancient origin of the yeast stage (NAGY et al. 2014). Therefore, it seems plausible that ancestral genetic resources have been utilized in similar ways in different lineages due to adaptations to the same environmental selection pressures. In case of the yeast stage, the emergence of this feature in different lineages is more likely related to change in regulatory mechanisms than to the occurrence of new genetic material (NAGY et al. 2014). In case of an ancient origin of the yeast, other obligate parasitic fungi (e.g. rust fungi and powdery mildews) seem to have lost this feature. Therefore, it is only natural to assume that the yeast stage serves a crucial function in the life history of lineages, with exception of some taxa in the Tilletiales, that exhibit the smut syndrome.

3. Anamorphic lineages and the consequences of the one fungus - one name concept

The haploid yeast stage poses two challenges for the scientists studying smut fungi. Firstly, smut fungi are mainly studied for their parasitic stage, and the yeast stage and its ecological role is an almost neglected field in the study of smuts (but see BREFELD 1881). Secondly, mainly with the advent of mole-

cular diagnostic methods it has become evident that several basidiomycetous yeasts belong to anamorphic lineages within Ustilaginomycotina and Microbotryales (e.g. Begerow et al. 2000, Wang et al. 2015a). This fact complicates the interpretation of adaptive evolution in these groups, as the smut syndrome, a central characteristic in previous interpretations of adaptive evolution, is lacking in purely anamorphic lineages.

The role of yeasts (also called sporidia) in the classical life cycle of smut fungi is well understood. Phragmobasidia germinating from teliospores subsequently produce four haploid basidiospores via meiosis. Thereby the two proximal and the two distal basidiospores have the same mating type, respectively. The basidiospores are able to reproduce mitotically by budding as yeasts. For infection of a susceptible host two haploid sporidia of opposite mating types need to fuse to produce an infection hyphae, which emerges from the zygote and infects the host plant. Most likely in order to increase the chances of fusion of haploid sporidia and infection, smut fungi in the Microbotryales and the Ustilaginomycotina have evolved an elegant reproductive system: intra-tetrade mating. This behaviour is best understood for *Microbotryum lychnidis-dioicae* (Hood & Antonovics 1998, 2000). Instead of producing basidiospores, compatible compartments of basidia germinating from teliospores can fuse directly to produce an infection hyphae (Schäfer et al. 2010). However, it has been shown *in vitro* that this behaviour is dependent on the available sugar content in the environment (Hood & Antonovics 1998). *In vivo*, it has been observed that intra-tetrad mating is dominant when teliospores were deposited on leaves of the host, where sugar contents are presumed to be low. In the flower however, where sugar contents are high, basidiospore germination and budding of yeasts is the predominant reproductive strategy (Schäfer et al. 2010). A tempting ecological interpretation is that the pollinator dispersal of teliospores to flowers increases chances of bringing together teliospores, respectively compatible sporidia, from several different individuals. Additionally, the favourable conditions within the flower nectar allow the fungus to delay the infection, as well as increase spore load by budding, which most likely increases the infection success. On leaves where spore deposition most likely is accidental and environmental conditions are less favourable, a strategy that leads to rapid infection will be advantageous. If similar mechanisms apply to species in the Ustilaginomycota is however not known.

The present knowledge in taxonomy of smut fungi will remain in a transitional stage, until a comprehensive integration of anamorphic and teleomorphic stages and taxa has been accomplished. Especially, the exploration of new environmental niches and the application of high-throughput DNA sequencing technologies will provide new and relevant data. In the meanwhile, key questions on the taxonomy of Ustilaginomycotina remain open: Which synapomorphies define Ustilaginomycotina? How to interpret traits currently seen as synapomorphies, such as the interaction apparatus (Bauer et al. 1997)? On

a more technical side, the question is of whether it is useful to include smut fungi in the the yeast standard literature (e.g. Kurtzman et al. 2011), and vice versa should yeast stages be included in smut fungal literature? How to emend traditional descriptions of teleomorphic taxa to include anamorphic species? These tasks are overdue and pose a challenge for the whole mycological community.

The integration and unification of formerly separated systems based on molecular data seems conceptually easy, but needs plenty of additional work at second view. Many taxa still await their molecular analysis and formal changes need taxonomic know-how which is declining (Rambold et al. 2013). However, the major challenge in our view will be a change in our way of thinking about smut fungal evolution. Smut fungi might be neither pure parasites nor pure yeasts, but true dimorphic lineages with two different ecologies. The integration of this concept will definitely add a further dimension in the understanding of smut fungal evolution.

4. The promise of genomics on the understanding of mechanisms of interaction

In the parasitic stage smut fungi gain their nutrients from their hosts and have evolved specialised interactions to obtain them (Bauer et al. 1997). Some lineages within the Ustilaginomycotina develop sophisticated morphological apparatuses to interact with their hosts, whereas the interaction of species in the Microbotryales does not result in such morphological differentiations. Genome sequencing of *Ustilago maydis* (Kämper et al. 2006), *Sporisorium reilianum* (Schirawski et al. 2010), *Ustilago hordei* (Laurie et al. 2012), *Melanopsichium pennsylvanicum* (Sharma et al. 2015) and *Microbotryum lychnidis-dioicae* (Perlin et al. 2015), thereby makes it possible for the first time to compare the molecular repertoire available for the two independently evolved lineages. Despite being plant parasites, the genomes of both lineages apparently only encode a surprisingly small amount of cell-wall degrading enzymes. This is interpreted as an adaptation to the biotrophic lifestyle of these fungi and their dependence on plant health to finish the smut life cycle. In both lineages, like in other plant-fungus systems, the interaction between parasite and host is mediated by secreted proteins. In the Ustilaginomycota (i.e. *U. maydis, S. reilianum* and *U. hordei*) many of these proteins are encoded in clusters in the genome and have been shown to be expressed in a host-tissue specific pattern (Skibbe et al. 2010). In *U. maydis*, the roles of secreted proteins that have been functionally characterized range from involvement in successful plant penetration (Doehlemann et al. 2009), manipulation of the host metabolism (Djamei et al. 2011), to sugar uptake by the fungus (Wahl et al. 2010). In *Microbotryum lychnidis-dioicae*, gene prediction indicates that the fungus has special enzyme sets for breaking down components commonly found in

pollen tubes and flowers, tissues were infection by the fungus is likely to take place. Additionally, the genome of *M. lychnidis-dioicae* encodes genes that are homologous to plant hormone synthesis genes (PERLIN et al. 2015). The possibility exists that the fungus uses these hormone pathways to establish itself in the anthers to replace the pollen with its spores during plant development. However, there is still need to experimentally confirm such mechanisms.

5. Current knowledge on the biogeography of smut fungi

The biogeography of most smut fungi is still barely understood, but principally it is accepted, that their distribution is congruent with the distribution area of the host species. Given the species richness of the Ustilaginomycotina, biogeography and distribution patterns in this group are understudied. Due to its relevance in agriculture and science, one of the first studies was probably the population study of *Ustilago maydis* (MUNKACSI et al. 2008). As expected, *U. maydis* occurs worldwide in all areas where corn is part of the regular food resources and roughly reflects the population structure of its host. All populations outside of the center of origin of *U. maydis* in Mexico were very similar to each other, except for a population in Brazil, which might be the result of a second lineage that followed the host out of Central America. An independent analysis of virulence genes revealed similar subpopulations (KELLNER et al. 2014). Thus, *U. maydis* confirms the hypothesis of parasites reflecting the distribution of the host and being almost present everywhere, where the host occurs – at least sooner or later.

Similar conclusions have been drawn from studies of *Microbotryum* and its hosts. Anther smut species of *Silene latifolia* and *S. dioica*, respectively, occur throughout the distribution range of their hosts in Europe. The parasite on *S. latifolia* thereby showed a congruent population structure with its host, having survived in the same or similar southern glacial refugia during the last ice age and co-migrated with the host. *Microbotryum* on *S. dioica* also showed striking biogeographic patterns, however, explanations for these were not as straightforward and might have included more northern glacial refugia (VERCKEN et al. 2010). Similar complexity was recently discovered for the geographic distribution of *M. silenes-acaulis*, where disease prevalence increased with increasing latitude (BÜKER et al. 2016). That the parasite can 'follow' its host, is also impressively demonstrated by the collections of *Microbotryum* in areas where the host has been introduced (ANTONOVICS et al. 2003). However, on a finer spatial scale the assumption of a complete overlap between host and parasite distribution might not be the case. Parasites are restricted to a sub-distribution of the host plant and their distribution is not exclusively dependent on host species, but also on other biotic as well as abiotic environmental factors. In the *Microbotryum-Silene* pathosystem it has been shown that in some environments that still permit the host to grow, the parasite is hardly

observed. *Microbotryum* on *Silene vulgaris* in the French Alps mainly occured at an altitude above 1300 m, whereas the host plant can be found below this altitude (ABBATE & ANTONOVICS 2014). The influence of elevation indicates abiotic factors correlated with altitudinal change. This study, as others before (ANTONOVICS et al. 1994), also found an influence of host population size. In general, many studies in the *Microbotryum-Silene* system show that the establishment and occurrence of persistent parasite populations is dependent on many factors and can not be explained solely by the occurrence of the host.

6. Is host specificity a key to understand evolution of smut fungi?

One striking feature of smut fungi is their high host specificity. An evaluation of VÁNKY's European Smut Fungi (1994) revealed that approx. 80 % of the species are infecting less than three different, often closely related species (BEGEROW et al. 2004). Early studies have even suggested to use smut fungi, amongst other plant parasites, as taxonomists to identify a plant species (NANNFELDT 1966). This certainly seems to be the case in some taxa. For instance *Laurus nobilis* from the Canary Islands is easy to be recognized by its infection with *Laurobasidium*. Likewise, some *Antherospora* species are highly specific and infect one host species only and might even indicate the relationship between hosts (PIĄTEK et al. 2011). However, many smut species are able to infect at least several, often closely related host species. Additionally, infection studies with *Microbotryum* spp. have shown, that even if a species has been reported from only a single host species in nature, it can infect related species under experimental conditions (e.g. DE VIENNE et al. 2009). A few instances of host jumps have even been discovered in natural settings (e.g. ANTONOVICS et al. 2002, KUMMER 2010). Similar observations have been reported for *Anthracoidea*, as so-called accidental infections. In this system, most likely the massive spore presence in a given location on one host species can lead to the infection of closeby plant species that is normally not parasitised by the respective *Anthracoidea* species (HENDRICHS et al. 2005).

Another characteristic of many smut fungal lineages is that monophyletic groups of smut fungi infect monophyletic lineages of host species. In addition to high host specificity this fact has led to the conclusion that co-speciation between host and parasite explains species diversity of smut fungi. In the Ustilaginomycotina there are only a few exceptions, like the Doassansiales, Microstromatales or Urocystales, where the different parasite genera are not restricted to a single host family. Their diversity is mostly explained as an adaptive radiation to a specific niche, such as aquatic or moist environments (BAUER et al. 1999). In recent years the view of co-speciation as the main explanation for phylogenetic patterns has been challenged by several studies on smut fungi. BEGEROW et al. (2004) revealed a principal difference

between *Microbotryum* on Caryophyllaceae and *Ustilago/Sporisorium* on Poaceae. Although both lineages are characterized by a certain degree of co-speciation events, the phylogeny of *Microbotryum* showed more congruence to the phylogenetic relationships of the different host genera. The phylogeny of *Ustilago/Sporisorium* on the other side might have resulted from frequent host jumps within each of the studied subfamilies of Poaceae (BEGEROW et al. 2004). The inclusion of more closely related taxa into co-phylogenetic studies of *Microbotryum* revealed a higher rate of host jumps in this group of smut fungi as well (REFREGIER et al. 2008). Recently, the genus *Anthracoidea* was analysed in a similar way and revealed a high degree of co-speciation with additional host jumps on closely related species (ESCUDERO 2015), as suggested by previous work (HENDRICHS et al. 2005). In the Entylomatales, monophyletic parasite lineages have colonized monophyletic host families and show a radiation within them (BEGEROW et al. 2002b). The sampling depth in this study was however not sufficient to support whether this was due to co-speciation or due to jumps to closely related hosts. Unpublished data on *Urocystis* (not shown), a genus infecting a broad variety of eu-dicot hosts shows a similar pattern. In a broader compilation of co-phylogenies of different plant parasitic groups a general rule in favour of one or the other colonization scenarios could also not be detected. While genera like *Exobasidium*, *Entyloma* and *Cintractia* reflect the diversification of their hosts, others like *Ustilago* and *Tilletia* seem to be more complex and host switching even between distantly related hosts is common (JACKSON 2004). Thereby, the results of such co-phylogenetic analyses are heavily dependent on taxon sampling as well as the resolution of the underlying phylogenies. Especially the more recent studies (REFREGIER et al. 2008, ESCUDERO 2015) with larger taxon sampling, indicate colonization scenarios for plant-parasitic smut fungal lineages, with the above-mentioned exceptions, as singular colonization events of a host lineage with subsequent radiation of this group via host jumps.

In addition to complex co-evolutionary mechanisms of host and parasite, a detailed comparison of *Microbotryum* on *Dianthus* and on *Silene*, respectively, revealed that host specificity can be rather different between sister lineages (KEMLER et al. 2013). Individual parasite species of *Silene* in general are restricted to one or a few host species, whereas parasite species of *Dianthus* can occur on many different hosts. It remains to be shown, if the higher degree of host jumps in *Dianthus* is a result of ongoing speciation in the host genus (VALENTE et al. 2010) or a lack of speciation in the parasite, but the patterns are significantly different between these two parasite sister groups.

The importance of some smut fungi in agriculture and science have led to the study of host interactions and the understanding of host specificity on genetic and molecular bases. While early genetic studies of *Ustilago maydis* focused on tumor induction and the infection process (KÄMPER et al. 2006, BREFORT et al. 2009), more recent studies incorporate comparative approa-

ches to understand host specificity of smut fungi. The analysis of the genome of *Sporisorium reilianum*, as *U. maydis* a parasite of maize, revealed high synteny to the *U. maydis* genome. The diverging regions in the *S. reilianum* genome were associated with an accumulation of secreted proteins involved in host-parasite interactions, most of which were homologous in both organisms and have evolved rapidly. Additionally, because of the species-specific secreted proteins the authors concluded that both organisms have evolved in parts to target different host molecules (Schirawski et al. 2010). *Ustilago hordei* showed a similar pattern of high synteny to the other two sequenced species, as well as diverging secreted proteins that most likely are adaptations to its specific host barley (Laurie et al. 2012). The latest addition of genomes of smut fungi in the Ustilaginaceae is *Melanopsichium pennsylvanicum*. It is a close relative of the abovementioned species, but instead of being a parasite of Poaceae and Cyperaceae like most Ustilaginaceae, it parasitizes members of the dicotyledon genus *Persicaria*. This species genomes also showed many secreted proteins unique to *M. pennsylvanicum* that are most likely involved in host interaction and adapted to this specific host. However, in contrast to the other Ustilaginaceae its effector protein genes are dispersed throughout the genome and not necessarily combined in gene clusters. There is no doubt that new genomic data in the Ustilaginomycotina will be obtained in the near future given the ability to get whole genome sequences at low costs and analytical power is increasing at the same time. Sequencing of *Microbotryum* species is still in its infancy compared to Ustilaginomycotina, but the recently published genome of *M. lychnidis-dioicae* opened up the possibilities to understand these fungi on a molecular level (Perlin et al. 2015). With respect to host specificity, it can be assumed that the already mentioned possible interference of the parasite with the hormone system of its host plays an important role. However, evidence for this is so far lacking, but new molecular methods such as the CRISPR-Cas9 system that has been successfully established for *U. maydis* (Schuster et al. 2016), might facilitate understanding on a molecular level for *Microbotryum* as well.

7. Conclusions

- Systematic and taxonomic concepts have improved significantly, but ongoing research emphasizes the preliminary nature of current classification.

- The integration of anamorphic lineages challenge our traditional view of Ustilaginomycotina and Microbotryales as exclusively plant parasitic lineages.

- Methodological advances reveal sophisticated molecular interactions that are distinct from other plant pathogens.

- Biogeography of smut fungi is shaped by host distribution as well as environmental factors.

- Host specificity does not necessarily result in co-speciation, but phylogenetic patterns are a result of frequent host jumps between closely related hosts, which are potentially facilitated by similar host or parasite physiologies.

- The comparison between Ustilaginomycotina and Microbotryales will reveal common and diverging patterns and will improve the understanding and control of smut fungi.

8. Acknowledgements

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