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REVIEW

Delimiting species in Basidiomycota: a review

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Abstract

Species delimitation is one of the most fundamental processes in biology. Biodiversity undertakings, for instance, require explicit species concepts and criteria for species delimitation in order to be relevant and translatable. However, a perfect species concept does not exist for Fungi. Here, we review the species concepts commonly used in Basidiomycota, the second largest phylum of Fungi that contains some of the best known species of mushrooms, rusts, smuts, and jelly fungi. In general, best practice is to delimitate species, publish new taxa, and conduct taxonomic revisions based on as many independent lines of evidence as possible, that is, by applying a so-called unifying (or integrative) conceptual framework. However, the types of data used vary considerably from group to group. For this reason we discuss the different classes of Basidiomycota, and for each provide: (i) a general introduction with difficulties faced in species recognition, (ii) species concepts and methods for species delimitation, and (iii) community recommendations and conclusions.

Keywords Biological species concept · Morphological species concept · Phylogenetic species concept · Taxonomy

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Table of contents

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Introduction

What is a species? This is one of the most fundamental questions in biology. Species are the basic units in biology, and can be defined as "separately evolving metapopulation lineages" as per de Queiroz (2007). Species are the way in which we categorize discrete and meaningful groups. Species concepts, in contrast to species, are the criteria used to delimit species. The pros and cons of different species concepts have been debated in numerous biological disciplines ranging from evolutionary biology to systematics and taxonomy. Numerous characteristics (or properties) displayed by organisms allow us to study species boundaries (i.e., the practical delimitation of species); species concepts such as the biological, morphological, ecological, and phylogenetic species concepts, should be regarded as ways to delimit species by placing emphasis on different criteria. At least 32 different species concepts have been identified (Mayden 1997; Wilkins 2009; Zachos 2016). Species concepts for Fungi have been recently reviewed in Lücking et al. (2020).

Although species are defined as separately evolving units, it is pertinent to point out that "plain" lineages are not always accepted as species, neither by some authors who explicitly stated so (e.g., Freudenstein et al. 2017) nor by the majority of researchers when some clear examples of single species with structured populations are presented (e.g., Jackson et al. 2017). The "separate and unitary evolutionary role and tendencies" from Simpson's (1951) definition, and the "role" emphasized by Freudenstein et al. (2017) thus are essential in our definition of species, despite often being difficult to apply in practice. Further, since evolution is continuous, it is inevitable to find borderline situations where phylogeographically structured populations of a single variable species and true recently diverged species may pose challenges to be distinguished (Huang 2020). And finally, some diversification patterns have been explained by an ephemeral speciation model, the idea being that incipient forms appear continuously within species but they rarely persist (Rosenblum et al. 2012).

Species delimitation criteria commonly used in Basidiomycota

The phenotype—understood as the set of morphological, anatomical, and biochemical traits, and even behavioral features and autoecology (Lücking et al. 2020)—is a highly complex expression of the genotype in a given environment (including epigenetic changes). The earliest species concepts in Fungi were based on the phenotype, mostly morphology (Micheli 1729; Linnaeus 1753; Persoon 1801; Fries 1821, 1829). In other words, organisms with different phenotypes were delimited as different species (Cronquist 1978). The phenotype provides a rich source of qualitative and quantitative characters to recognize species, although analytical approaches are uncommon in Basidiomycota beyond the direct comparison of descriptive traits (Zamora et al. 2015). However, there are a number of problems with this species concept in Fungi. First, phenotypes may exhibit a variable extent of plasticity, which makes it untenable for this criterion to be used as the only one in species delimitation and recognition. Second, many fungal organisms, especially single-celled taxa such as the yeasts, typically display a limited set of taxonomically useful morphological characters, due to their relative simplicity (Boekhout et al. 2021). In addition, their rate of morphological change is slower (Taylor et al. 2006a, b).

It could be argued that more in-depth studies lead to unearthing subtler albeit more reliable characters for species delimitation, but a negative relationship was suggested between the number of studied specimens and clear species boundaries by Yao and Li (2016). The main limitation of a phenotype-based species delimitation is the existence of morphologically close species, of which intra- and interspecific variation amply overlap regarding some characters that have been traditionally used to separate taxa. These species are referred to as "cryptic", a concept that was already mentioned by Mayr (1942) as "sibling species". Nowadays, there is a tendency of distinguishing a number of related concepts, often following Mann and Evans (2007), such as (i) pseudocryptic species, which do have reliable morphological differences but are so similar that they are often difficult to be identified; (ii) semicryptic species, which can be recognized only if other phenotype-related characters, such as ecology and distribution, are also used; and (iii) strictly cryptic species that are truly indistinguishable based on morphological traits. It is hardly imaginable, although debatable, that truly cryptic species could exist, but in practice some may be effectively indistinguishable based on the phenotypic characters studied so far. This problem is well-known in some groups of Basidiomycota, and one of the classic examples is the morphospecies *Armillaria mellea* (sensu lato), which contains over a dozen species as determined by mating tests (Hintikka 1973; Anderson and Ullrich 1979; Men et al. 2016).

Reproductive isolation is often used to delimit fungal species. Eriksson (1950) was the first to perform interfertility tests in corticioid fungi, followed by, e.g., Hallenberg (1983a, 1988) and Hallenberg et al. (1996). In Agaricales, this approach has been relatively common, and potential reproductively isolated species have been detected in many groups (Boidin 1986; Lamoure 1989; Petersen 1995a, b; Aanen and Kuyper 1999, 2004). *Heterobasidion* (Russulales) is another example of a genus in which biological species recognition has been applied when morphological characters do not support separation of species (Niemelä and Korhonen 1998). However, in vitro experiments have indicated that *Heterobasidion* species retain between 5 and 98% interfertility, depending on the species combinations (Garbelotto and Gonthier 2013). Hybridization processes in nature have also been repeatedly documented to occur between pairs of taxa within the *H. annosum* species complex (Garbelotto and Gonthier 2013; Sedlák and Tomšovský 2014; Sillo et al. 2019). Both hybridization and genetic isolation happen in pathogenic yeasts of the genus *Cryptococcus* (Boekhout et al. 2021). Some other studies have suggested hybridization to occur in other groups, for example *Malassezia* (Theelen et al. 2004; Wu et al. 2015) and other members of Ustilaginomycotina (Kellner et al. 2011). There are some limitations in using intercompatibility tests (Hallenberg 1987): (i) uniparental or homothallic species are excluded, limiting the number of studied species; (ii) the number of available cultures from geographically distinct locations and different substrates

is restricted; (iii) the results are not easily interpreted and negative mating tests may not always imply that two species belong to different compatibility groups; and (iv) intercompatibility as proof of conspecifity is to some extent artificial. Another limitation is that fungi of specialized ecological guilds, such as ectomycorrhizal (ECM) taxa, are often not culturable.

The use of genealogies or phylogenies to study species delimitation is also relatively old. Eldredge and Cracraft (1980) and Cracraft (1983) focused species recognition on this criterion, defining species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent". Phylogenies can be inferred using a variety of characters, including phenotypic data and DNA characters, or a combination of both. Since one of the main characteristics of speciation events is the interruption of the gene flow among groups of individuals (Coyne and Orr 2004), it should be possible to assess species boundaries by analyzing the genetics of the organisms involved. The simplest of the DNA-based methods aimed at delimiting species is barcoding, which consists of the use of one or few short DNA regions with low intra-specific variation and high inter-specific variation (Hebert et al. 2003). The most frequently used region for barcoding purposes in fungi is the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA (Schoch et al. 2012), although other regions may be selected as secondary or alternative barcodes (Stielow et al. 2015). DNA barcoding, however, is unreliable for species recognition in a number of taxa—including *Crepidotus*, *Hohenbuehelia*, *Laccaria*, *Mucidula*, and *Phaeocollybia* (Badotti et al. 2017), the *Hypholoma fasciculare* complex (Sato et al. 2020), *Mycena* sect. *Calodontes* (Harder et al. 2013), and *Pluteus* sect. *Pluteus* (Justo et al. 2014). It is therefore better regarded as a tool for helping with species identification rather than for species descriptions. Even when proper species delimitation analyses are applied to single-locus phylogenies, e.g., by using GMYC (Pons et al. 2006) or PTP (Zhang et al. 2015), qualities such as paralogy (including the presence of several unconcerted copies in multicopy regions; Aime et al. 2017), lack of variation in recent radiations, recombination, incomplete lineage sorting, hybridization, horizontal gene transfer, et cetera (Dupuis et al. 2012; Zamora et al. 2018) all negatively affect the accuracy of analyses and, thus, the reliability of the results.

Genealogical Concordance Phylogenetic Species Recognition (GCPSR) was proposed by Taylor et al. (2000) as a more advanced approach for species delimitation. It relies on the use of several unlinked DNA regions (recombination should not occur within a region) to build up single-region phylogenies, of which tree topology concordance is then assessed. Species are considered the minimum units above which there are no incongruences among single-locus phylogenies. Below the level of species, intra-specific incongruences among the genetic information contained in the loci are expected as a result of recombination among individuals. This approach unfortunately does not account for any of the many situations that lead to incongruences even among well-defined species, such as the presence of shared ancestral polymorphisms, introgression, hybridization, et cetera. In these cases, if strictly applied, GCPSR could undersplit species so severely that higher-level taxa with well-known problems of incongruences among loci would fall into the definition of a single species (e.g., Cantharellales; Moncalvo et al. 2006). This may look as an extreme example that no taxonomist would accept, but incongruences among phylogenies tend to become more common in closely related species (e.g., due to deep coalescence), which are precisely the targets of most species delimitation analyses. On the other hand, this method is prone to oversplitting in cases where structured populations are present, since tree topologies of a few loci likely agree following a phylogeographical pattern.

Finally, coalescence-based species delimitation analyses are among the most powerful methods based on phylogenetic data, implemented in software such as SpedeSTEM (Ence and Carstens 2011), BP&P (Yang and Rannala 2014), and STACEY (Jones 2017). Here, species boundaries are inferred not directly based on single-locus trees, but using an estimated species tree that accounts for incongruences caused by the presence of shared ancestral polymorphisms (incomplete lineage sorting). These analyses have become more standard in mycology, although the number of studies using them in Basidiomycota is still low (e.g., Svantesson et al. 2019; Zamora and Ekman 2020). Given enough variation in the data, these methods are prone to oversplitting. It has been demonstrated that they can treat structured populations as species (Sukumaran and Knowles 2017) because they detect population rather than species splits (Leaché et al. 2019). In addition, coalescence analyses are unappropriate in cases of reticulate evolution, including hybridization, introgression, and horizontal gene transfer, since those situations violate the assumptions of the model. The multispecies network coalescent (Yu et al. 2014) has been developed to deal with these situations, inferring species networks instead of dichotomous phylogenies, although how to translate the output to putative species may still be challenging. On the other hand, the use of hundreds or thousands of loci obtained through next-generation sequencing (NGS) and good analytical pipelines could also overcome some of the aforementioned problems.

All species delimitation approaches have strengths and shortcomings, and there is not a single method able to reliably identify all species (Carstens et al. 2013). Regarding this,

it is important to remember that the output of any of these analyses are not "species", but "candidate" or "putative" species or lineages, which should be critically evaluated in light of available data before proposing taxonomic treatments. Therefore, approaches combining as many taxonomic sources of information as possible, i.e., an integrative (or polyphasic) taxonomy approach (Dayrat 2005), account for most accuracy. In this paper, we discuss species delimitation within Basidiomycota by higher taxonomic group (sensu He et al. 2019; Wijayawardene et al. 2020) and present for each a review of methods for species delimitation and community recommendations for future work on this subject.

Subphylum Agaricomycotina

Species delimitation in Agaricomycetes

Agaricomycetes (~ 30,143 species) encompasses the majority of described species in Basidiomycota and includes 22 orders, 128 families, and 1434 genera (He et al. 2019). In Agaricomycetes, the pileate-stipitate morphotype is dominant, along with the coralloid, polyporoid, corticioid, gasteroid, and other forms, and the group includes saprotrophs, pathogens, and mutualists (Hibbett et al. 2014). Sánchez-García et al. (2020) highlighted that morphological transitions, not nutritional modes, are the most important drivers of diversification across Agaricomycetes and that lineages with pileate-stipitate basidiomata have strongly increased diversification rates across all clades. As a result of the complexity of morphological and ecological diversity, there are many difficulties in the delimitation of Agaricomycetes species. Regarding DNA-based molecular methods, ITS is still the most widely used region for identifying species within Agaricomycetes. There is an increasing tendency to combine multiple loci with the ITS region (Stielow et al. 2015; Tekpinar and Kalmer 2019). The most comprehensive phylogenetic analyses of Agaricomycetes so far were a multilocus and genomic-scale data-based phylogeny of 5284 taxa (Varga et al. 2019) and a five-locus analysis of 8472 taxa (Sánchez-García et al. 2020). Given the extreme diversity contained within Agaricomycetes, we will introduce practices regarding species delimitation for higher clades within the class.

Species delimitation in Agaricales

The order Agaricales, typified with the genus *Agaricus*, encompasses most of the so-called mushrooms and toadstools and is one of the best studied and conspicuous morphologically varied assemblage of Agaricomycetes (Singer 1986; Hibbett et al. 1997, 2014; Hibbett 2007; Zhao et al. 2008; Kalichman et al. 2020). Agaricales is by far the largest and diverse order in Fungi with 23,225 described species (Kirk 2019) distributed in 46 families and 509 genera (Kalichman et al. 2020). Agaricales is also the fungal order with most species described in recent years (Cheek et al. 2020). In addition, Agaricales is one of the youngest orders in Basidiomycota, with recent estimates dating the origin of this order between 135 and 173 million years ago (He et al. 2019; Varga et al. 2019; Sánchez-García et al. 2020). Most Agaricales are saprotrophic or form mutualistic symbioses with a great variety of vascular plants (ectomycorrhizae). Others are plant pathogens, facultative human pathogens (e.g., *Schizophyllum commune*), fungal pathogens (e.g., *Rhodophana stangliana*, *Squamanita* spp.), predators on nematodes (e.g., *Hohenbuehelia*, *Pleurotus*), and—mainly in the tropics—symbiotic partners of green algae, cyanobacteria, and insects. Although less common, Agaricales species are also found in freshwater, marine, and mangrove habitats.

In terms of basidiomata, the pileate-stipitate forms with lamellate (gilled) hymenophores are dominant (343 genera, accounting for 67% of total generic diversity), along with the secotioid and gasteroid sequestrate forms, including false truffles, puffballs, and bird's nest fungi and, to a lesser extent, resupinate, clavarioid, cyphelloid, and pileate with poroid hymenophores (Zhao et al. 2008; Hibbett et al. 2014; Kalichman et al. 2020; Põlme et al. 2020). Molecular studies have revealed that characters such as basidioma formation and habit, hymenophore type, and color of spore-print were traditionally overemphasized (Singer 1986; Horak 2005) and are not reliable phylogenetic markers at higher taxonomic level, having resulted in many artificial groups (Hibbett et al. 1997; Hibbett 2007, 2014; He et al. 2019; Varga et al. 2019; Sánchez-García et al. 2020). While some nongilled resupinate, cyphelloid, aphyllophoralean, and gasteroid fungi should be included in Agaricales (Hibbett et al. 1997; Bodensteiner et al. 2004; Binder et al. 2005, 2010; Matheny et al. 2006a, b; Sulistyo et al. 2021), the opposite is also true—some typical pileate-stipitate gilled mushroom occur in other orders of Agaricomycetes: *Lactifluus*, *Lactarius*, *Lentinellus*, *Multifurca*, and *Russula* in Russulales (Miller et al. 2006; Buyck et al. 2008); *Erytrophylloporus*, *Hygrophoropsis*, *Paxillus*, *Phylloporopsis*, *Phylloporus*, and *Tapinella* in Boletales (Binder and Hibbett 2006; Farid et al. 2018; Vadthanarat et al. 2019b); and *Contumyces*, *Gyroflexus*, and *Rickenella* in Hymenochaetales (Larsson et al. 2006). Automated searches of the NCBI GenBank and MycoCosm databases by Kalichman et al. (2020) found that 7% of generic names of Agaricales had DNA sequences of

their type specimens, 68% had sequences of their type species, 87% of genera were represented by sequences (non-type), and 103 accepted genera lacked sequence data.

Species concepts and species recognition

Species identification in Agaricales has traditionally relied on morphological characters (e.g., Singer 1986; Bas et al. 1988; Horak 2005; Knudsen and Vesterholt 2008) that are known to be subject to parallel evolution and phenotypic plasticity (Slepecky and Starmer 2009). In many cases, separation of species based on morphology alone is challenging and many taxa represent complexes with (pseudo)cryptic species (Geml et al. 2006; Bickford et al. 2007; Carriconde et al. 2008; Stefani et al. 2014; Balasundaram et al. 2015; Guo et al. 2016; Sánchez-García et al. 2016; Li et al. 2017; Peintner et al. 2019; Vizzini et al. 2019a, b; Nilsen et al. 2020; Sato et al. 2020; Voitk et al. 2020). Putative interspecific hybridization events have been suggested to occur in some Agaricales (Aanen et al. 2000; Hughes et al. 2013).

Mycelial compatibility groups studies have been used for species delimitation (Lamoure 1974, 1989; Boidin 1980, 1986; Petersen 1995a, b; Petersen et al. 1999) within various saprotrophic and ECM genera, such as *Agrocybe*, *Armillaria, Coprinus, Flammulina, Gymnopus, Hebeloma, Hypholoma, Laccaria, Lentinula*, *Marasmius*, *Marasmiellus*, *Omphalina*, *Omphalotus*, *Pholiota*, *Pleurotus*, *Psathyrella*, *Stropharia*, alone or usually coupled to morphological (phenotypic) and/or molecular analysis (e.g., Lamoure 1974, 1989; Kemp 1975; Romagnesi 1975, 1982; Korhonen 1978; Anderson et al. 1980; Guillamin and Berthelay 1981; Vilgalys and Miller 1983, 1987; Jacobsson 1986, 1987, 1989, 1990; Jahnke et al. 1988; Flynn and Miller 1990; Mueller 1991; Mueller and Gardes 1991; Vilgalys 1991; Petersen 1992, 1995a, b; Petersen and Hughes 1993, 1998; Murphy 1997; Petersen et al. 1999; Aanen and Kuyper 1999, 2004; Nicholl and Petersen 2000; Zervakis et al. 2004; Mata et al. 2004; Lechner et al. 2005; Qin et al. 2007; Wannathes et al. 2007; Uhart and Albertó 2009; Ravash et al. 2010). Culture studies have proved useful for delimiting taxa in *Lyophyllum* sect. *Difformia* (Moncalvo et al. 1993).

The study of the number of nuclei present inside the basidiospores has proved useful to discriminate species in *Hygrocybe* and *Lepiota* (Kühner 1980; Vellinga and Huijser 1998; Vizzini et al. 2014a, b). Isozyme analysis is rather efficient for determining variation in fungi (Micales et al. 1986; Bonde et al. 1993) and has been widely used in the identification of species in some genera of Agaricales, such as *Armillaria* (Wahlström et al. 1991; Agustian et al. 1994), *Flammulina* (Alekhina et al. 2001), and *Pleurotus* (Magae et al. 1990; Zervakis and Labarere 1992; Zervakis et al. 1994, 2001). A rapid methodology for the identification of Agaricales via protein profiling based on matrix-assisted laser desorption/ionization mass spectrometry (MALDI-TOF MS) was proposed by Sugawara et al. (2016). Zervakis et al. (2012) successfully applied the Fourier transform infrared (FT-IR) spectroscopy for taxa delimitation within the genus *Pleurotus*.

Non-sequence-based molecular methods have been used alone or in support of molecular analyses, including DNA–DNA hybridization (reassociation) (Jahnke 1985, 1987; Jahnke and Bahnweg 1986; Jahnke et al. 1987, 1988), DNA profiling techniques, e.g., restriction fragment length polymorphism (RFLP) (Castle et al. 1987; Smith and Anderson 1989; Gardes et al. 1990; Mueller and Gardes 1991; Bunyard et al. 1996; Anderson et al. 1998; Methven et al. 2000; Hughes et al. 2001; Urbanelli et al. 2007; Carriconde et al. 2008; Meza-Meneses et al. 2016; Kondo et al. 2017), amplified fragment length polymorphism (AFLP) (Lee et al. 2000; Kim et al. 2006; Urbanelli et al. 2007; Ota et al. 2012), random amplified polymorphic DNA (RAPD) (Hsiang and Wu 2000; Zervakis et al. 2001; Stott et al. 2005; Alam et al. 2010), cleaved amplified polymorphic sequences (CAPS) (Stott et al. 2005), and analyses of SSRs/microsatellites (Carriconde et al. 2008; Vincenot et al. 2017; Wang et al. 2018).

Regarding sequence-based molecular methods, ITS is still the most widely used marker for species identification within Agaricales (Badotti et al. 2017; Yang et al. 2018; Vu et al. 2019; Kalichman et al. 2020). It is quite easy to amplify and sequence, even from old specimens—up to 200 years old (Larsson and Jacobsson, 2004; Liimatainen et al. 2014, 2020; Nilsen et al. 2020). ITS has been found to be a suitable barcode for some groups in the Agaricales, including the genera *Amanita* (e.g., Vizzini et al. 2016b; Cui et al. 2018; Saba et al. 2019; Hanss and Moreau 2020), *Cortinarius* (e.g., Frøslev et al. 2005, 2007, 2017; Liimatainen et al. 2014, 2020; Stefani et al. 2014; Garnica et al. 2016; Nilsen et al. 2020), *Entoloma* (Dima et al. 2021), *Gymnopilus* (Thorn et al. 2020), *Hebeloma* (Eberhardt et al. 2013), *Lepista* (Wang et al. 2019), *Marasmius* (Shay et al. 2017; Haelewaters et al. 2020a), *Melanoleuca* (Vizzini et al. 2011; Antonín et al. 2014, 2015, 2017), *Tricholoma* (Jargeat et al. 2010; Heilmann-Clausen et al. 2017), *Tricholomopsis* (Holec and Kolařík 2012; Cooper and Park 2016), and the families Agaricaceae (Justo et al. 2015; Vizzini et al. 2014a, b, 2019a, b), Lyophyllaceae (Bellanger et al. 2015), and Hygrophoraceae (Ainsworth et al. 2013; Lodge et al. 2014; Lücking et al. 2017; Larsson et al. 2018; Voitk et al. 2020). On the other hand, ITS-based phylogenies have low resolution for species recognition in *Crepidotus*, *Hohenbuehelia*, *Laccaria*, *Mucidula*, and *Phaeocollybia* (Badotti et al. 2017), the *Hypholoma fasciculare* complex (Sato et al. 2020), *Mycena*

sect. *Calodontes* (Harder et al. 2013), and *Pluteus* sect. *Pluteus* (Justo et al. 2014).

There is a general tendency towards combining multiple loci with the ITS region (Stielow et al. 2015; Tekpinar and Kalmer 2019; Lücking et al. 2020). Other loci used in Agaricales for combined analyses include the intergenic spacer region (IGS) (Liang et al. 2011; Wang et al. 2019), nuclear small and large subunit rRNA genes (SSU, LSU) (e.g., Sánchez-García et al. 2016; Vizzini et al. 2015, 2020; Oliveira et al. 2019; Saba et al. 2019, 2020; Varga et al. 2019), mitochondrial SSU (mtSSU) (e.g., Liang et al. 2011; Eberhardt et al. 2013; Grilli et al. 2016; Wang et al. 2019; Saba et al. 2020), mitochondrial ATP synthase protein subunit 6 (*atp6*) (Robison et al. 2001; Kluting et al. 2014; Baroni et al. 2020; Jian et al. 2020), cytochrome oxidase 1 mitochondrial gene (*cox1*) (Damon et al. 2010; Dentinger et al. 2011), the largest and second largest subunits of RNA polymerase II (*rpb1* and *rpb2*, respectively) (e.g., Frøslev et al. 2005; Harder et al. 2013; Qin et al. 2014; Antonín et al. 2015, 2017; Cui et al. 2018; Wang et al. 2018; Baroni et al. 2020; Olariaga et al. 2020; Mešić et al. 2021), translation elongation factor 1-α (*tef1*) (e.g., Jargeat et al. 2010; Ota et al. 2012; Harder et al. 2013; Justo et al. 2014; Wang et al. 2019; Corrales et al. 2020; Vizzini et al. 2020), β-tubulin (*btub*) (e.g., Geml et al. 2006; Nagy et al. 2012; Qin and Yang 2016; Cui et al. 2018; Fraiture et al. 2019), glyceraldehyde-3-phosphate dehydrogenase (*gpd*) (Nuytinck et al. 2007; Ota et al. 2012; Stefani et al. 2014), a *m*acro*e*volutionary *g*enomic marker specific to *B*asidiomycota (*megB1*) (Babasaki et al. 2007; Ota et al. 2012), nitrate reductase (*nar*), glucose-6-phosphate dehydrogenase (*g6pd*) (Vincenot et al. 2012), and the gene coding for the Minichromosome Maintenance Complex Component 7 (*Mcm7*) (Eberhardt et al. 2013; Stefani et al. 2014). Finally, for species delimitation in *Flammulina*, Wang et al. (2018) used homeodomain1 of the mating gene (HD1-A).

In addition, incorporation of secondary structural information of ribosomal sequences in phylogenetic analysis has been shown to increase the accuracy and robustness of phylogenies (Landis and Gargas 2007; Ahvenniemi et al. 2009; Zhang et al. 2015; Yang et al. 2018; Sundaresan et al. 2019). In particular, exploring the secondary structure of the ITS2 spacer region for *Tricholoma* (Suk and Kim 2002) and "Lycoperdaceae" (Krüger and Gargas 2008), and of mtSSU for *Agrocybe* (Gonzalez and Labarère 1998; Uhart et al. 2007), and *Pleurotus* (Gonzalez and Labarère 2000) has been a promising approach in species delimitation.

Conclusion and recommendations

ITS remains an important barcode marker to delimit species. In many groups of Agaricales, ITS may be sufficient to discriminate among species, whereas other (cryptic) taxa require secondary barcoding markers or multilocus analyses. Besides ITS, the most employed markers are LSU, *rpb1*, *rpb2*, *tef1*, *btub*, and *atp6*. An integrative taxonomy approach is strongly encouraged for species delimitation in Agaricales. A prime example is that by Lodge et al. (2014) on Hygrophoraceae, in which multilocus phylogenetic data are integrated with information from morphology, pigment chemistry, and ecology. Finally, sequencing of old herbarium type specimens (even over 100 years of age) with Sanger or next-generation sequencing approaches has proven feasible in members of Ascomycota and Russulales (e.g., Forin et al. 2018, 2020; Delgat et al. 2019; Kistenich et al. 2019; Gómez-Zapata et al. 2021) and should be attempted in Agaricales.

Species delimitation in Amylocorticiales

Amylocorticiales is a small order with about fifty species distributed in ten genera (Binder et al. 2010; He et al. 2019), including mostly resupinate forms such as *Amylocorticiellum*, *Amylocorticium*, *Amyloxenasma*, *Ceraceomyces*, and *Serpulomyces*, but there is considerable morphological diversification within the group. Non-resupinate members include the 'pagoda fungus', *Podoserpula pusio*, which has a multi-tiered pileate-stipitate form; and sister taxa *Irpicodon pendulus* and *Plicaturopsis crispa*, which are pileate-sessile. *Plicaturopsis* and *Podoserpula* both have merulioid hymenophores; *Irpicodon* has an irregularly hydnoid hymenophore; and *Anomoloma* and *Anomoporia* have poroid hymenophores. All species in Amylocorticiales have a monomitic hyphal system with clamped hyphae and a thickening hymenium. Basidiospores are invariably smooth, allantoid, cylindrical or ellipsoid with thin to thickened spore walls; most corticioid species have amyloid spore walls. Cystidia are not common and when present, they are simple, tube-like, sometimes septate. Amylocorticiales was identified as an independent group within Agaricomycotina by Larsson (2007) but only recognized as an order by Binder et al. (2010). Most species of the Amylocorticiales are thought to be saprotrophic and occur on wood at various stages of decay, mostly causing a brown rot. There is diversity in the mode of decay, however.

Species concepts and species recognition

Usually, species of corticioid fungi have been delimited based mainly on morphology and chemical reactions of hyphae and basidiospores, but also using substrate preference information, and compatibility mating tests. Among the resupinate forms of Amylocorticiales, which share a

monomitic hyphal system and usually lack cystidial elements, basidiospore thickness and reactions to iodine are useful characters (Eriksson and Ryvarden 1973; Zmitrovich and Spirin 2002; Bernicchia and Gorjón 2010; Gorjón et al. 2011).

Because morphological characters are limited, molecular phylogeny and phylogenomics are often employed to elucidate species and species complexes. Few recent phylogenetic studies deal with Amylocorticiales. Song et al. (2016) studied phylogenetic relationships of *Anomoloma* and *Anomoporia* but the order needs further studies in delimitation of (genera and) species.

Conclusion and recommendations

A satisfactory approach to discriminate species of Amylocorticiales requires the integration of morphological features, biochemical reactions, sequence data, nuclear behavior, mating compatibility, decaying abilities, ecological strategies, and host preferences (Larsson 2007; Rajchenberg 2011). Whereas LSU is the locus of choice for higher taxonomic level relationships, the ITS region should be used for the study of genera, species complexes, and species (Larsson 2007; Nilsson et al. 2008; Song et al. 2016). It may also be useful to incorporate *tef1* in addition to ITS; *tef1* provides better resolution in separating species (Carlson et al. 2014; Miettinen et al. 2018). The *rpb2* gene is more variable than *tef1* and recovers higher taxonomic clades with support (Matheny et al. 2007).

Species delimitation in Atheliales

The order Atheliales comprises five families (Atheliaceae, Byssocorticiaceae, Lobuliciaceae, Pilodermataceae, and Tylosporaceae), approximately 20 genera, and about 100 described species of mostly corticioid fungi (Sulistyo et al. 2021). Over the years, several genera have been described and added to Atheliales, based on morphological characters alone (Hjortstam and Ryvarden 2010) or combined with molecular phylogenetic evidence (Kotiranta et al. 2011). Sequence-based studies found some of these genera to be polyphyletic, sometimes with members clustering within other orders (Hibbett et al. 2007; Ertz et al. 2008; Binder et al. 2010; Sulistyo et al. 2021). Members of Atheliales are generally inconspicuous and possess few diagnostic features, including pellicular basidiomata, thin-walled hyphae in a monomitic hyphal system, rarely with cystidia, which, if present, are little differentiated (Eriksson and Ryvarden 1973; Larsson 2007; Bernicchia and Gorjón 2010). Despite a simple morphology, members of Atheliales are remarkably diverse in their ecological strategies; the order includes ECM, white rot saprotrophic, lichenicolous members, and a species that is a putative parasite of termites.

Species concepts and species recognition

There are few reliable characters to separate genera and species based on morphology alone. Also, most species of the largest genus in the order, *Athelia* (32 species; Wijayawardene et al. 2020), are regarded as siblings—for example, species limits within the *Athelia epiphylla* complex are not yet clarified (Eriksson and Ryvarden 1973; Bernicchia and Gorjón 2010; Sulistyo et al. 2021). Sulistyo et al. (2021), who presented an order-wide multilocus phylogenetic analyses, found a number of genera to be non-monophyletic: *Amphinema*, *Athelia*, *Athelopsis*, and *Leptosporomyces* (Sulistyo et al. 2021). Few DNA sequences are available, and as a result several of the lower taxonomic taxa are in need of revision.

An interesting situation occurs in the family Tylosporaceae. The phylogenically close relationship of *Amphinema* and *Tylospora* (sensu Sulistyo et al. 2021) is surprising when considering the differences in morphology. *Amphinema* is the only genus of Atheliales with conspicuous cystidial elements and smooth basidiospores, whereas *Tylospora* has lobed and ornamented basidiospores. Members of the two genera form ECM associations. Both *Amphinema* (Sulistyo et al. 2021) and *Tylospora* (Tedersoo and Smith 2013) are non-monophyletic. It is clear from the several taxonomic problems highlighted by Sulistyo et al. (2021), but also by the low phylogenetic resolution retrieved on key nodes was low, that more sampling needs to happen to decipher generic and species limits.

Conclusion and recommendations

Future studies of Atheliales should incorporate sequence data for genera of Atheliales sensu lato that were not included in the order-wide study by Sulistyo et al. (2021): *Athelicium*, *Athelocystis*, *Butlerelfia*, *Elaphocephala*, *Hypochniciellum*, *Melzericium*, and *Mycostigma*. For delimitation of genera and species, molecular-based studies on ITS, LSU, *rpb2*, and *tef1* are necessary. Finally, given the remarkable diversity observed in the order, Atheliales is a model group to study evolutionary patterns of nutritional modes. However, more sampling is needed, including from tropical areas, to improve phylogenetic resolution.

Species delimitation in Boletales

The order Boletales encompasses species commonly known as fleshy pored mushrooms or boletes. They are a globally distributed and extraordinarily diverse assemblage with about 2173 described species (Kirk 2019) placed in 16 families and 141 genera (He et al. 2019), including the fossil genus *Palaeogaster* (Poinar et al. 2014). The numbers of

species and genera are likely to be higher because many tropical and subtropical areas are still poorly sampled. The majority of the thus far described species taxa (77%) are characterized by a pileate-stipitate habit with tubulose hymenophore (Binder et al. 2010; Hibbett et al. 2014). Other species have above- or belowground, sequestrate, gilled agaricoid or pleurotoid, corticioid, or polyporoid habits (Høiland 1987; Agerer 1999; Binder and Hibbett 2006; Watling 2008; Jarosch 2001; Nuhn et al. 2013; Hibbett et al. 2014; Wu et al. 2014, 2016; He et al. 2019).

Most genera in the Boletales are ECM associates of a large variety of conifers (gymnosperms) and broadleaved trees (angiosperms) (Newman and Reddell 1987; Binder and Hibbett 2006; Rinaldi et al. 2008; Tedersoo et al. 2010). Recently, *Scleroderma* turned out to be a putative orchid endomycorrhizal symbiont in Mexico (Gonzáles-Chávez et al. 2018). In the case of some gall-forming species belonging to Boletinellaceae (*Boletinellus merulioides* and *Phlebopus* spp.), they appear to establish symbiotic relations with mealy bugs and aphids (Brundrett and Kendrick 1987; Nuhn 2016; Fang et al. 2020). A few genera in Boletales may be mycoparasitic; *Chroogomphus* and *Gomphidius* (Gomphidiaceae) are able to parasite rhizomorphs and ectomycorrhizae of the closely related *Rhizopogon* (Rhizopogonaceae) and *Suillus* (Suillaceae) (Miller 1964; Agerer 1990, 1991, 2006; Olsson et al. 2000); *Buchwaldoboletus*, *Chalciporus*, and *Pseudoboletus* (Boletaceae) are parasitic on members of other genera of Boletales or other Agaricomycetes (*Amanita*, *Phaeolus schweinitzii*, *Scleroderma*; Binder and Hibbett 2006; Nuhn et al. 2013). Few Boletales are saproxylic wood-rotting species inhabiting decayed stumps, fallen twigs or branches, and dead standing trees preferably of conifers and exclusively producing a Coniophoraceae-type brown rot (Nilsson and Ginns 1979; Besl et al. 1986; Jarosch 2001). Some genera are able to colonize building structures such as wooden timber, cottages, and porous bricks (corticioid genera as *Coniophora*, *Leucogyrophana*, *Serpula*), which are among the most dangerous wood-destroying fungi (Gilbertson 1981; Schmidt et al. 2002; Mattsson et al. 2010; Skrede et al. 2011; Hyde et al. 2018).

Binder and Hibbett (2006) provided the first comprehensive molecular study of Boletales using a combined analysis of four loci (5.8S, LSU, mtLSU, *atp6*). Six clades were recognized at the subordinal level: Boletineae, Coniophorineae, Paxillineae, Sclerodermatineae, Suillineae, and Tapinellineae. Nuhn et al. (2013) analyzed the generic and sub-generic relationships in Boletineae; using a combined LSU, *rpb1*, and *tef1* dataset, they identified 17 clades within four major groups and transferred Paxillaceae to Boletineae. Based on the analysis of a combined LSU, *rpb1*, *rpb2*, and *tef1* dataset, Wu et al. (2014) recovered 59 genus-level clades in Boletaceae distributed over seven major clades, six out of which have been recognized as monophyletic subfamilies: Austroboletoideae, Boletoideae, Chalciporoideae, Leccinoideae, Xerocomoideae, and Zangioideae. The seventh major clade remained largely unresolved in the analysis and was provisionally named as "*Pulveroboletus* group".

Species concepts and species recognition

Species identification in Boletales has traditionally relied on morphological characters associated to the basidioma (e.g., Watling 1970, 2008; Engel 1983; Engel et al. 1983, 1996; Singer 1986; Watling and Li 1999; Bessette et al. 2000, 2016; Lannoy and Estadès 2001; Horak 2005, 2011; Muñoz 2005; Watling and Hills 2005; Noordeloos et al. 2018). Mycelial compatibility studies (Fries 1985; Fries and Neumann 1990; Sen 1990), cultural data (Hutchinson 1991), and isozyme analysis (Sen 1990) have been sometimes used for species delimitation. Schmidt and Kallow (2005) used MALDI-TOF MS for identification of mycelia of wood-decay fungi as *Coniophora putena*, *C. marmorata*, *Serpula lacrymans*, and *S. himantioides*. DNA profiling techniques have been used alone or combined with sequencing studies, including RFLP (Bresinsky 1996; Anderson et al. 1998; Jasalavich et al. 2000; Hitchcock et al. 2003; Leonardi et al. 2005; Marques and Muñoz 2006; Sanon et al. 2009; Dunham et al. 2013), T-RFLP (Råberg et al. 2005), AFLP (Kauserud et al. 2006; Skrede et al. 2012), ARDRA (Schmidt and Moreth 1998a, 1999), RAPD (Anderson et al. 1998; Junghans et al. 1998; Schmidt and Moreth 1998b), and analyses of SSRs/microsatellites (Hitchcock et al. 2003; Kretzer et al. 2003).

Regarding sequence-based molecular methods, ITS is still the most widely used marker in species delimitation within Boletales (Badotti et al. 2017). ITS is a reliable barcode marker for species in several genera, e.g., *Astraeus* (Phosri et al. 2014), *Chroogomphus* (Scambler et al. 2018; Kiran et al. 2020), *Phylloporus* (Neves et al. 2012), *Rhizopogon* (Sulzbacher et al. 2016), *Suillellus* (Vizzini et al. 2014c), *Suillus* (Kretzer et al. 1996; Wu et al. 2000; Manian et al. 2001; Nguyen et al. 2016), *Xerocomellus* (Frank et al. 2020), and *Xerocomus* (Taylor et al. 2006a, b, 2007), but a poor marker in other genera (e.g., *Butyriboletus*, *Pisolithus*; Badotti et al. 2017). Some genera in Leccinoideae (*Leccinum*, *Octaviania*, *Rossbeevera* and *Turmalinea*) are characterized by a minisatellite-like insertion within the ITS region (den Bakker et al. 2004; Orihara et al. 2012). Orihara et al. (2016) pointed out that the insertion sequences within the ITS2 spacer of *Rossbeevera* and *Turmalinea* are highly informative and can be used as a unique molecular barcode.

Cryptic speciation is present in many genera, including *Astraeus* (Phosri et al. 2014), *Paxillus* (Hedh et al. 2008; Jargeat et al. 2014, 2016), *Pisolithus* (Martin et al. 2002), *Rhizopogon* (Dowie et al. 2017), *Serpula* (Carlsen et al. 2011; Balasundaram et al. 2015), and *Strobilomyces* (Sato

et al. 2007). Balasundaram et al. (2015) and Tremble et al. (2020) questioned the employment of the ITS locus alone in separating cryptic species in Boletales. In particular, Balasundaram et al. (2015) suggested using ITS only in combination with other loci, after pointing out that *btub*, *hsp*, *rpb2*, and *tef1* loci are more informative than ITS at the species level (even in single-locus trees). Interspecific hybridization events have been documented in *Coniophora* (Kauserud et al. 2007), *Leccinum* (den Bakker et al. 2007), and *Octaviania* (Orihara et al. 2021).

The more commonly used loci in combined analyses in Boletales (besides ITS) are SSU, 5.8S, LSU, *atp6*, *cox1*, *cox3*, mtSSU, mtLSU, *rpb1*, *rpb2*, *tef1*, *gdp*, *Gapdh*, *btub*, and *hsp*, and a combination of *actA*, *gpiA*, *hydA*, *rabA*, and *btub* (Kretzer and Bruns 1999; Peintner et al. 2003; den Bakker and Noordeloos 2005; den Bakker et al. 2007; Beugelsdijk et al. 2008; Hedh et al. 2008; Dentinger et al. 2010, 2011; Li et al. 2011; Skrede et al. 2011; Neves et al. 2012; Wilson et al. 2012; Gelardi et al. 2013, 2015; Moreau et al. 2013; Jargeat et al. 2014, 2016; Phosri et al. 2014; Wu et al. 2014, 2016, 2018; Zhao et al. 2014a, b; Balasundaram et al. 2015; Sato and Hattori 2015; Trappe et al. 2015; Henkel et al. 2016; Orihara et al. 2016; Raspé et al. 2016; Davoodian et al. 2018, Farid et al. 2018; Song et al. 2019; Vadthanarat et al. 2019a, b; Varga et al. 2019; Frank et al. 2020; Haelewaters et al. 2020a; Han et al. 2020; Kuo and Ortiz-Santana 2020; Liu et al. 2020; Sánchez-García et al. 2020; Orihara et al. 2021). Dowie et al. (2017), using ten anonymous nuclear loci (ANL), produced a phylogeny of *Rhizopogon* subgenus *Amylopogon* with much greater resolution than the one based on ITS alone.

Conclusion and recommendations

Species delimitation ideally rests upon an integrative approach, integrating—as already mentioned for Agaricales—morphological features, cultural characteristics, mycelial compatibility studies, pigments and secondary metabolites composition, sequence data, ecological strategies, and host preferences. The ITS is the marker of choice for species identification. In case of species complexes, it is suggested to use a combination of *rpb1*, *rpb2*, *tef1*, *atp6*, *cox3*, and *gpd* (Matheny et al. 2007; Jargeat et al. 2014, 2016; Gelardi et al. 2015; Davoodian et al. 2018; Farid et al. 2018; Vadthanarat et al. 2019a, b; Varga et al. 2019; Han et al. 2020; Kuo and Ortiz-Santana 2020). Strongly supported phylogenies and reliable species delimitation analyses can be obtained by combining several (unlinked) loci (Wu et al. 2014, 2016; Sato et al. 2017; Sato and Toju 2019). An impressive example of a multilocus analysis was recently published by Sato et al. (2017), where a phylogenetic reconstruction inferred from sequences of 80 single-copy genes of the ECM *Afroboletus* and *Strobilomyces* suggested that host-shift events, particularly those dealing with Fagaceae/Pinaceae, can provide ecological opportunities for a burst in the diversification of the two fungal genera.

Species delimitation in Corticiales

Corticioid fungi in the wide sense are a highly polyphyletic group of fungi with resupinate basidiomata as synapomorphic character. The term corticioid derives from *Corticium*, a crust-like genus, and the name is usually referred to resupinate homobasidiomycetes, with a variable hymenial configuration, from smooth to poroid forms. Gorjón (2020) compiled and keyed out the 420 accepted genera of corticioid fungi. Resupinate forms occur in every major clade of Agaricomycetes (Hibbett and Binder 2002; Larsson et al. 2004; Larsson 2007), and in this work they are considered in all treated orders. Corticioid fungi may have evolved repeatedly through reduction from erect forms (Hibbett and Thorn 2001; Larsson et al. 2004) or, alternatively, they may represent the ancestral form of basidiomata (Hibbett and Binder 2002; Binder et al. 2005; Sánchez-García et al. 2020). The order Corticiales sensu stricto currently contains about 120 species in 26 genera and four families (Corticiaceae, Dendrominiaceae, Punctulariaceae, Vuilleminiaceae).

Despite being simple in macro- and micromorphology, taxa of Corticiales show considerable ecological and nutritional diversity, including saprotrophic, lichenicolous, plant pathogenic, and lichenized lineages inhabiting diverse types of substrata (Ghobad-Nejhad et al. 2010). The group is characterized by basidiospores with pink-colored walls, which is evident in a spore print. Many species develop a catahymenium with probasidia deeply sunken in a dense layer of dendrohyphidia as an adaptation to desiccation (Larsson 2007).

Species concepts and species recognition

Genera and species in the Corticiales have been delimited based on multiple features: basidioma morphology, microscopic features such as presence or absence of cystidial elements and shape and size of basidiospores, mating tests, habit and nutritional mode, host preferences, and geographical distribution.

Corticium and related genera *Dendrocorticium* and *Dentocorticium* have been extensively studied based on morphological characters and host preference data (Boidin and Lanquetin 1983; Duhem and Michel 2008, 2009; Larsen and Gilbertson 1974, 1977; Larsen and Nakasone 1984); DNA sequences are lacking for most species and phylogenetic relationships are unresolved.

Species identification in the decorticant corticioid *Vuilleminia* has been based primarily on host identification, spore size, and cystidial configuration. According to Ghobad-Nejhad et al. (2010), however, spore size and host

specificity are not so critically important factors for delimiting species of *Vuilleminia* compared to ITS sequences. However, the heterogeneous nature of the *Vuilleminia comedens* group with respect to spore size and shape is not fully reflected only by ITS sequence data.

Conclusion and recommendations

The ITS divergence between some species in the Corticiales (e.g., *V. comedens* and *V. coryli*, about 2.0–2.2%) is lower than the average value for intraspecific variation in Basidiomycota (sensu Nilsson et al. 2008). Most phylogenetic analyses in Corticiales have been based on ITS and LSU (Ghobad-Nejhad et al. 2010; Ghobad-Nejhad and Duhem 2014). For studies within species complexes and to delimit species, the recommended approach is using a combination of ITS, LSU, *tef1*, *rpb1*, and *rpb2* and integrate morphological features, biochemical reactions, mating compatibility tests, decaying abilities, ecological strategies, and host preferences.

Species delimitation in Geastrales

Geastrales is an order in the Phallomycetidae, comprising exclusively gasteroid and primarily saprotrophic fungi (Hosaka et al. 2006). Rhizomorphs are typically conspicuous, with generative hyphae bearing some ampullaceous septa, and certain species develop a notorious mycelial subiculum on the substrate. Basidiomata are either stellate at maturity or sequestrate, the peridium is bi- to pluristratificate, with a ± membranous endoperidium, and basidia often bear more than four basidiospores, which are inamyloid, nondextrinoid, symmetric, and centrally attached to the sterigmata (Sunhede 1989; Hosaka et al. 2006). The order was originally defined to accommodate earthstar-like genera with a powdery glebal mass (*Geastrum* and *Myriostoma*, Kreisel 1969), and only later expanded to its current circumscription, with the inclusion of Sclerogastraceae (Hosaka et al. 2006; Hosaka and Castellano 2008). Geastrales contains about 160 species in six genera (*Boninogaster*, *Geastrum*, *Myriostoma*, *Schenella*, *Sclerogaster*, *Sphaerobolus*) and four families (Geastraceae, Schenellaceae, Sclerogastraceae, Sphaerobolaceae). *Geastrum* is, by far, the most species-rich genus, with probably more than 130 species (Zamora et al. 2014a; He et al. 2019).

Systematics in Geastrales have been based on morphological features until the last decades. Genera are well-defined based on phenotypic characters, although molecular data have played a decisive role to assess the placement of some sequestrate taxa, for example the current acceptance of *Radiigera* as a sequestrate form of *Geastrum* (Jeppson et al. 2013; Zamora et al. 2014a). The generic boundaries among *Boninogaster* and *Sclerogaster* are still not completely solved (Hosaka and Castellano 2008), while the identification of *Myriostoma*, *Schenella*, and *Sphaerobolus* at generic level does not represent a particular challenge. Problems for species delimitations are, however, numerous. *Geastrum* includes several widely recorded species that most likely represent species complexes (e.g., *G. pectinatum*, *G. saccatum*, *G. schweinitzii*, *G. striatum*) (see Zamora et al. 2015; Accioly et al. 2019). The systematics of the genus *Sphaerobolus* has been revised in Geml et al. (2005) and that of *Myriostoma* in Sousa et al. (2017).

Species concepts and species recognition

Most species of Geastrales can be recognized based on detailed morphological studies. Different sets of characters are used for each genus. Macromorphologically diagnostic traits include basidioma development (hypogeous, epigeous), dehiscence (stellate, irregular, indehiscent), number of peridial layers (e.g., in *Geastrum* and *Sphaerobolus*), presence or absence of subiculum, ability of the external mycelial layer to encrust debris (*Geastrum*), ornamentation of the endoperidium (*Geastrum*, *Myriostoma*), presence or absence of stalk(s) and their morphology (*Geastrum*), presence of a peristome and its ornamentation (*Geastrum*, *Myriostoma*), organization of the glebal mass (chambered or not in *Sphaerobolus*, forming peridioles of various sizes and persistency in *Schenella*), color of the glebal mass (*Geastrum*, *Sclerogaster*), general basidioma habit, size, and color, among others. Micromorphological characters include basidiospore morphology (shape, size, ornamentation, including scanning electron microscope studies), presence or absence of gemmae (*Sphaerobolus*), capillitium features, morphology of the cells in different parts of the fruitbody (e.g., thin- or thick-walled in the pseudoparenchymatous layer of *Geastrum*, or protruding hyphae on the endoperidial surface), and crystalline deposits on the endoperidial body (*Geastrum*). The morphology of rhizomorph crystals proved to be of great importance to separate species groups in *Geastrum*, as well as macrochemical spot tests with reagents detecting phenoloxidase activity (Zamora et al. 2013). The use of statistical analyses is infrequent, but clustering analyses were used in Zamora et al. (2013) and morphometrics in Zamora et al. (2014b, 2015).

The first phylogenies focusing on species-level taxonomy in Geastrales were based on LSU (Douanla-Meli et al. 2005), but soon included multilocus approaches combining the ITS, LSU, and *atp6* (Hosaka and Castellano 2008; Kasuya et al. 2012). Jeppson et al. (2013) published the first phylogeny on European species of *Geastrum* using ITS, LSU, *atp6*, and *tef1*, and Zamora et al. (2014a, b, 2015) used concatenated datasets of ITS, LSU, *atp6*, and *rpb1* sequences in their worldwide phylogeny of *Geastrum* and species delimitation studies in *G.* sect. *Schmidelia* and *G.* sect. *Geastrum*.

Conclusion and recommendations

Much work is needed on species delimitation in Geastrales, particularly in the genera *Geastrum* and *Sclerogaster*. The many old species names, for which sometimes there is not original material left, will inevitably delay the resolution of some species complexes, until the identity of all relevant names is settled. Particularly challenging groups are species complexes in *Geastrum* involving, e.g., *G. javanicum*, *G. lageniforme*, *G. saccatum*, and *G. triplex*, for which worldwide-based monographs are required. The current general trend in the group is to split rather than to synonymize taxon names (Jeppson et al. 2013; Zamora et al. 2015; Sousa et al. 2017; Accioly et al. 2019), and most species described in the last decade have both phenotypic, ecological, biogeographical, and molecular associated data—the recommended approach. Importantly, old taxon names should be investigated in detail (including type studies whenever possible) before proposing nomenclatural changes, as this will avert the publication of redundant names for already described species. Given the complexity of the fruitbodies in some species, studying sufficient well-preserved specimens will prevent defective/flawed descriptions that may introduce confusion in the literature. Finally, the analysis of unlinked DNA loci will contribute to robust phylogenies and well-supported species delimitation analyses, overcoming the limitations of single-locus approaches.

Species delimitation in Gloeophyllales

The order Gloeophyllales, with about 50 known species in 13 genera, contains a morphologically diverse array of polypores (*Gloeophyllum* s.l.), agarics (*Neolentinus*, *Heliocybe*), and resupinate fungi (*Veluticeps*, *Boreostereum*, *Chaetodermella*), most of which are demonstrated to produce a brown rot mode of wood decay and are found preferentially on coniferous substrates (García-Sandoval et al. 2011). Relationships within the Gloeophyllales are important to understanding the evolution of brown rot fungi in Agaricomycotina. Phylogenies of Gloeophyllales have been performed using sequences of SSU, 5.8S, LSU, *rpb2*, *tef1*, and *atp6* (García-Sandoval et al. 2011). Species-level phylogenetic studies have thus far been based on combined ITS–LSU datasets (He and Li 2013; He et al. 2014).

Species concepts and species recognition

Species, and also genera, of Gloeophyllales can usually be recognized based on morphological characters. There are few agaricoid forms, and important characters for resupinate and polyporoid lineages are presence/absence of a well-developed pilear surface and hymenophore configuration, which varies from smooth to poroid with round or daedaloid to lamellate pores. Most species in Gloeophyllales have cystidial elements that are of importance to delimit species. Some generic limits within Gloeophyllales are uncertain. For example, *Heliocybe* and *Neolentinus* are either placed in synonymy (Rune 1994) or treated as two genera (García-Sandoval et al. 2011) and *Campylomyces* and *Pileodon* are segregates of *Veluticeps* that have yet to be included in phylogenetic analyses (Nakasone 2004). *Gloeophyllum* in the wide sense includes a dozen species with variable hymenophore configuration. The genus is polyphyletic (García-Sandoval et al. 2011) and He et al. (2014) proposed to use the previously introduced genera *Griseoporia* and *Osmoporus* and erected *Hispidaedalea* to accommodate several species previously in *Gloeophyllum*.

Conclusion and recommendations

A combination of morphology and molecular phylogenetic data is suggested for continued species delimitation in Gloeophyllales. Species have thus far only been discriminated based on nuclear ribosomal DNA (rDNA) sequences (ITS, LSU). For example, the resupinate genus *Veluticeps* with about ten species worldwide has only been studied using the ITS region (He and Li 2013). Usually, species of *Veluticeps* and related taxa are well defined by morphological characters (Nakasone 2004). However, widely distributed species, such as *V. berkeleyi* that has been reported from North America, Europe, and eastern Asia, may represent species complexes. The ITS region do not provide sufficient variation to resolve such complexes in Gloeophyllales, and protein-coding genes such as *rpb2*, *atp6*, and *tef1* should be tested for their efficacy in delimiting species (Gorjón and Bernicchia 2010; S.P. Gorjón, unpubl. data).

Species delimitation in Gomphales

Gomphales (sensu Jülich 1981) is a monophyletic order of Agaricomycetes, informally known as gomphoid fungi (Jülich 1981; Hibbett and Thorn 2001; Hosaka et al. 2006; Giachini et al. 2010; Hibbett et al. 2014). The order includes species with different basidioma morphologies including coral-shaped (e.g., *Phaeoclavulina, Ramaria, Ramaricium*, Lentariaceae), club-shaped (Clavariadelphaceae), gilled (*Gloeocantharellus*), cantharelloid-gomphoid (e.g., *Gomphus*, *Phaeoclavulina*, *Turbinellus*), tooth-like (*Beenakia*), resupinate-odontoid (*Hydnocristella* and *Kavinia*), and sequestrate (Gautieriaceae) (Pine et al. 1999; Villegas et al. 1999; Humpert et al. 2001; Hosaka et al. 2006; Giachini et al. 2010; Hibbett et al. 2014). Despite their macromorphological variations, the members of this clade share a number of microscopic and macrochemical characters, including cyanophilic spore ornamentation, chiastic basidia, hyphal construction, and positive hymenial reaction to ferric sulfate

(Donk 1964; Villegas et al. 1999). Ecologically, the order includes saprotrophic, lignicolous, and ECM taxa.

Species concepts and species recognition

Species delimitation based on morphological characteristics is heavily depending on genus. The presence or absence of clamp connections (Corner 1950, 1966, 1970), cyanophilic reaction of basidiospores to cotton blue (Kotlaba and Pouzar 1964), and spore ornamentation (Marr and Stuntz 1973) are the most important morphological characteristics to separate species within *Ramaria*. In *Gomphus*, *Phaeoclavulina*, and *Turbinellus*, basidioma characteristics (color, shape, size, habitat, overall aspect), size and ornamentation of basidiospores, and hyphal construction (clamped, non-clamped, branching pattern) provide the best results in species delimitation. In some genera, like *Clavariadelphus*, staining reactions to KOH, $FeCl_3$, and NH_4OH are informative for species recognition (Methven 1990; Huang et al. 2020), whereas for *Beenakia, Hydnocrystella* and *Kavinia*, basidiospore shape, ornamentation, and size as well as fruiting body morphology are generally useful to disciriminate at the species level (Nuñez and Ryvarden 1994; Chen et al. 2015; Robledo and Urcelay 2017). Even though informative, morphological characters alone are in most cases insufficient for accurate species delimitation in Gomphales.

Several molecular markers have been designed, tested, and established to identify species within Gomphales: SSU, LSU, mtSSU, *rpb2*, *tef1*, and *atp6* (Vilgalys and Hester 1990; White et al. 1990; Kretzer and Bruns 1999; Pine et al. 1999; Humpert et al. 2001; Giachini 2004; Hosaka et al. 2006; Giachini et al. 2010; Knudson 2012; Maneevun et al. 2012). For some taxa, it is also possible to use the ITS barcode for species delimitation, but its use varies greatly among genera (Giachini 2004; Knudson 2012; Maneevun et al. 2012; Huang et al. 2020).

Conclusion and recommendations

Accurate species delimitation relies upon the combination of morphological, ecological, biochemical, and molecular phylogenetic data. This integrative approach is necessary; many species share similar morphological traits, which makes it difficult to make species-level identifications. Taxa such as *Ramaria flava*, which is frequently cited in the literature, present problems of conceptualization and are frequently considered in a very broad sense often contradicting the original description of the taxon. Species such as *R. sanguinea*, *R. vinosimaculans*, and many more are possibly being hidden under an incorrect name (Estrada-Torres 1994). Species of *Phaeoclavulina* face the problem of different fruiting body morphologies that can easily place species within *Ramaria*. *Gomphus* and *Turbinellus* also share very similar macromorphological characters that tend to put species into either one of the genera by the untrained eye. *Kavinia* and *Hydnocristella* are hard to identify and separate due to the inconspicuous format of basidiomata, just to name some of the major challenges.

Species delimitation in Hymenochaetales

Hymenochaetales is a large order of Agaricomycetes, with over 900 species and more than 80 currently recognized genera, placed in six families (Coltriciaceae, Hymenochaetaceae, Oxyporaceae, Repetobasidiaceae, Schizoporaceae, Tubulicrinaceae). The order is dominated by wood-inhabiting saprotrophs and trunk rot parasites causing white rot (e.g., *Hyphoderma, Hyphodontia, Inonotus* s.l., *Phellinus* s.l., *Rigidoporus, Trichaptum, Tubulicrinis, Xylodon*), ECM symbionts (*Coltricia*, *Coltriciella*), and bryophyte-associated agarics (*Loreleia*, *Rickenella*). There is a large variation in basidioma morphology including polyporoid, poroid, corticioid, stereoid, hydnoid, agaricoid, clavarioid, corraloid, and fan- to funnel-shaped.

Species concepts and species recognition

Traditionally, the following characters have been crucial for species delimitation based on morphology: size and shape of basidiomata, basidiospores, setae, and cystidia. Delimitation of species based on morphology alone is not recommended, because many taxa harbor cryptic species complexes (e.g., *Fomitiporia*, *Phellinus igniarius* group, *Porodaedalea*). Analyses of DNA content, sexuality pattern (homothallic vs. heterothallic), and mating tests were applied in studies in *Inonotus* s.l. and *Phellinus* (Fischer 1987, 1994). In parasitic taxa, the host spectrum is considered to be informative for species delimitation (Fischer and Binder 2004; Tomšovský et al. 2010a, b; Zhou et al. 2016a, b; Wu et al. 2018). RFLP also helped to understand relationships among species in the *Phellinus igniarius* group or within *Porodaedalea* (Fischer 1996; Fischer and Binder 1995). Whereas genera of Hymenochaetales are generally separated using LSU-based phylogenies, the most connomly used marker for species delimitation is the ITS barcode (Fischer and Binder 2004; He and Li 2012; Vlasák and Vlasák 2017). Recent studies usually employ the ITS in combination with other markers. Combination of the ITS and LSU loci is the most common approach applied in analyses of *Coniferiporia* and *Phellinidium* (Zhou et al. 2016a, b), *Fomitiporia* (Liu et al. 2018), *Fulvifomes* (Salvator-Montoya et al. 2018), *Lyomyces* (Yurchenko et al. 2017), *Phellinotus* (Drechsler-Santos et al.2016), *Rigidoporus* (Wu et al. 2017), *Sidera* (Miettinen and Larsson 2011), and *Xylodon* (Riebesehl et al. 2019). Combination of the ITS and *tef1* markers are applied in identification of species in *Hydnoporia* (Miettinen et al.

2019), *Phellinus* s.s. (Tomšovský et al. 2010b; Zhou et al. 2016a, b), and *Porodaedalea* (Tomšovský et al. 2010a; Wu et al. 2018). The phylogenetic reconstruction of four-locus datasets of ITS, LSU, *rpb2*, and *tef1* sequences has been applied in *Fomitiporia* (Amalfi et al. 2014; Campos Santana et al. 2014; Alves-Silva et al. 2020) and *Porodaedalea* (Brazee and Lindner 2013), whereas a combined SSU, 5.8S, LSU, and *rpb2* dataset is employed in the taxonomic study of *Hyphoderma* and *Lawrynomyces* (Salcedo et al. 2020).

Conclusion and recommendations

Most of the numerous taxonomic studies of Hymenochaetales that were recently published are focused on Hymenochaetaceae. Knowledge about the other families is limited. Especially corticioid and odontoid genera such as *Hyphoderma*, *Hyphodontia*, *Kneiffiella*, *Lyomyces*, *Peniophorella*, *Tubulicrinis*, and *Xylodon* deserve more monographic treatments based on morphology and multilocus phylogeny. Some genera within Hymenochaetaceae also deserve more study—for example, DNA sequences are lacking for *Clavariachaete*. Similar to other orders of Agaricomycetes, a polyphasic approach incorporating data from morphology, ecology, biogeography, and multilocus phylogenetic analyses is suggested. Multilocus datasets should not only include sequences of ITS and LSU, but also of protein-coding genes (*tef1*, *rpb1*, *rpb2*). Also data of sexuality pattern, genome size, and ploidy level are helpful for accurate taxonomy. In the case of species complexes, the diversification is often associated with host specificity and geographic distribution (Tomšovský et al. 2010a, b; Zhou et al. 2016a, b). In these highly divergent parasitic taxa, intragenomic ITS polymorphisms repeatedly decrease the quality of ITS sequences. For example, in the genus *Porodaedalea*, phylogenies based on ITS–*tef1* and a four-locus dataset (ITS, LSU, *rpb2*, *tef1*) have been unable to resolve the taxonomy of the "*Porodaedalea* holarctic group" (Brazee and Lindner 2013) and "*Porodaedalea* spp. 3 and 4" (Wu et al. 2018). A genome-wide genotyping method (e.g., AFLP, ddRADseq) would be useful to study speciation processes dependent on biogeographic pattern and host association.

Species delimitation in Jaapiales

Jaapiales is the smallest order of Agaricomycetes including a single corticioid genus, *Jaapia*, with two species, *Jaapia argillacea* and *J. ochroleuca*. Both *Jaapia* species produce thin, fully resupinate basidiomata and function as saprotrophs growing in very wet wood. Analyses of nuclear and mitochondrial rDNA genes (Binder et al. 2005) placed *Jaapia* as the sister group of the rest of Agaricomycotina, but analyses of the LSU alone (Larsson 2007) resulted in *Jaapia* being a close relative of Corticiales, Gloeophyllales, and Thelephorales.

Species concepts and species recognition

Members of the order are characterized by adnate, effused, smooth basidiomata, by the monomitic hyphal system with clamped hyphae and tubular, projecting, thick-walled cystidia, and by the fusiform strongly cyanophilous basidiospores (Eriksson and Ryvarden 1976; Bernicchia and Gorjón 2010). The two species *Jaapia argillacea* and *J. ochroleuca* are well separated by differently shaped thick-walled basidiospores. The phylogenetic analysis of an ITS dataset revealed two clades that correspond to the two described species (Telleria et al. 2015).

Conclusion and recommendations

There are no species delimitation problems in Jaapiales. The separation of the two known species is confirmed by both morphology and phylogenetic studies. Based on the results of Telleria et al. (2015), we recommend the ITS as the barcode for future studies of species delimitation in this small order.

Species delimitation in Polyporales

Polyporales is a well-supported monophyletic clade (Matheny et al. 2007). The order contains 3553 described species (Kirk 2019), placed in 292 genera and 19 families (Wijayawardene et al. 2020). The great majority of these are lignicolous saprotrophs, whereas a few are plant pathogens and root parasites (Binder et al. 2013). Members of Polyporales are frequently isolated as endophytes from woody tissues and roots (Martin et al. 2015; Duan et al. 2019) and some of them (*Microporus*, *Physisporinus*) form mycorrhizal associations with orchids (Ogura-Tsujita et al. 2018; Yamashita et al. 2020). A wide variety of basidioma types exist in Polyporales, including perennial conks (e.g., *Laricifomes*) and pileate-stipitate, effused-reflexed or resupinate forms. A few species produce multiple flabelliform lobes (e.g., *Hydnopolyporus*, *Sparassis*), *Cryptoporus volvatus* has a unique poroid basidioma that is enclosed by a subtended volva (Park et al. 2014), and *Lentinus tigrinus* has a typical agaricoid basidioma with lamellate hymenophore (Hibbett et al. 1994). The hymenophore is mainly poroid in Polyporales, but can also be hydnoid, merulioid, or smooth (Hibbett et al. 2014). Several species in the order have an asexual stage (Stalpers 1984, 2000) and some form subterranean sclerotia (Smith et al. 2015; Wu et al. 2020a).

Species concepts and species recognition

Species identification in Polyporales has traditionally relied on macro- (e.g., basidioma shape, pilear and hymenial surface) and micromorphological characteristics (e.g., hyphae, hyphal system, cystidia, basidia, basidiospores). However, characteristics differ for each taxon, and these concepts have changed over time according to subjective aspects. The genus *Ganoderma*, the largest genus in Polyporales with about 180 species (He et al. 2019), is probably the most expressive example for this problem. Morphology-dependency has resulted in ambiguous species circumscriptions in *Ganoderma* (Lloyd 1905; Ryvarden 1991; Papp et al. 2017). Since the DNA era, several molecular markers have been used to clarify species boundaries within the genus: IGS, SSU, ITS, LSU, mtSSU, *btub*, *rpb1*, *rpb2*, *tef1*, and *atp6* (Moncalvo et al. 1995; Hong and Jung 2004; Sun et al. 2006; Zheng et al. 2009; Wang et al. 2012; Thakur et al. 2015; Zhou et al. 2015; Loyd et al. 2018; Xing et al. 2018). Recently, when new *Ganoderma* species are described, they are almost exclusively supported by multilocus phylogenies incorporating sequences from rDNA loci as well as from protein-coding genes (*tef1*, *rpb1*, *rpb2*) (e.g., Liu et al. 2019; Luangharn et al. 2019; Tchotet Tchoumi et al. 2019; Ye et al. 2019; Wu et al. 2020c). In addition to morphological observations and molecular phylogenetic analyses, metabolic profiling has been suggested in species delimitation (Richter et al. 2015).

Several DNA-based studies have reported remarkable species diversity within previously recognized morphospecies—including *Antrodia* spp. (Spirin et al. 2015a, 2016a, 2017), *Ceriporia purpurea* (Spirin et al. 2016b), *Jahnoporus hirtus* (Spirin et al. 2015b), *Laetiporus sulphureus* (Lindner and Banik 2008; Song et al. 2014, 2018), *Skeletocutis nivea* (Korhonen et al. 2018), *Sparassis crispa* (Hughes et al. 2014), and *Wolfiporia cocos* (Wu et al. 2020a). One of the most striking examples of hidden species diversity revealed by molecular phylogenetic studies was observed in *Cyanosporus* (previously: *Postia caesia* complex). This genus forms a distinctive morphological group, which contains closely related brown-rot polypore species, characterized by blue-tinted basidiomata, curved, weakly cyanophilous, and greyish basidiospores, and amorphous aggregates (Miettinen et al. 2018; Shen et al. 2019). Before molecular methods became available, mating tests, macroscopic characteristics (e.g., the structure of upper surface, size and color of basidiomata), and basidiospore width were proposed as main features for species delimitation within the complex (David 1974, 1980; Corner 1989; Rajchenberg 1995; Ryvarden 1988; Niemelä et al. 2001; Pieri and Rivoire 2005; Papp 2014, 2015). However, morphology-based species was not confirmed by the early phylogenetic studies (e.g., Yao et al. 2005; Ortiz-Santana et al. 2013; Pildain and Rajchenberg 2013). Only recently, multilocus phylogenetic analyses have revealed unexpected species diversity in the complex (Miettinen et al. 2018; Shen et al. 2019; Liu et al. 2021). Nevertheless, the separation of cryptic species is difficult based on morphology alone, and DNA sequences are required for reliable delimitation. The ITS barcode is the most widely used molecular marker but does not have enough discriminatory power in some taxa. For example, *Cyanosporus fusiformis* and *C. ungulatus* differ in their ITS only by 1 nucleotides (nt), and *C. mongolicus* and "*Postia*" *auricoma* differ only by 2 nt. It is noteworthy that based on a polymorphic ITS sequence of a collection from Russia, Miettinen et al. (2018) inferred interspecies hybridization within *Cyanosporus alni* and "*Postia*" *populi*, further complicating the delimitation of species in *Cyanosporus*. Among other molecular markers, only *tef1* sequences are widely available for the species in *Cyanosporus* (Miettinen et al. 2018). The *tef1* gene is in general more variable between species than ITS and provides greater resolution in separating species; for example, ITS sequences vary only between 1 and 6 nt between species in the *C. alni* clade, whereas variation in *tef1* is between 9 and 32 nt (Miettinen et al. 2018). *Cyanosporus* is currently one of the most difficult genera of Polyporales for species delimitation and the use of ITS alone is often insufficient.

In addition to molecular phylogenetic analyses and morphological study of basidiomata and mycelia, Peintner et al. (2019) studied growth characteristics, carried out enzyme assays, and comparatively analyzed volatile compounds in order to resolve cryptic species in *Fomes fomentarius* s.l. These authors found that the hymenophore pore diameter and the diameter of skeletal hyphae are taxonomically valuable features if measured from statistically relevant structures. Furthermore, they found that the content of volatile organic compounds as well as the mycelial characteristics in pure culture (e.g., daily mycelial growth rates, temperature range of pure cultures) are promising features for reliable species delimitation. Cultural characteristics and mycelial compatibility tests have long been used for species delimitation in Polyporales (e.g., Nobles 1948, 1965; David 1974; Stalpers 1978; Hallenberg 1988; Rajchenberg 1995). As an example, different strains of *Phlebia livida* were recognized to be incompatible in mating tests by Hallenberg (1988). Hallenberg and Larsson (1993) suggested that the *Phlebia livida* complex consists of two incompatible subspecies. Later, Ghobad-Nejhad and Hallenberg (2012a, b) proposed that the two subspecies be raised to species rank based also on morphology, phylogenetic analysis of an ITS dataset, haplotype network of the ITS1 spacer region, and substrate preference.

Conclusion and recommendations

Historically, species recognition in Polyporales was mostly based on examination of morphological characteristics,

which are often subjective or highly variable (e.g., in *Ganoderma*). These problems have been circumvented by the introduction of approaches based on DNA sequencing of conserved genomic regions. The ITS quickly became the most widely applied barcoding marker in Polyporales. For many genera in the order, the ITS is an appropriate marker for species delimitation and can be successfully sequenced from historical herbarium type specimens (Papp and Dima 2018). However, the ITS barcode is not equally variable in all Polyporales; it provides insufficiently resolution to allow correct identification of certain fungal groups (e.g., within the *Postia caesia* complex). Phylogenetic reconstructions of multilocus datasets are recommended, in combination with detailed micro- and macromorphological examinations, biological studies (mating tests), ecological strategy, and biogeography. An excellent study for such an integrative taxonomic approach is provided by Haight et al. (2019) on the *Fomitopsis pinicola* complex in North America.

Species delimitation in Russulales

Within Russulales, one of the largest orders in Agaricomycota with an estimated 4000 species, Russulaceae is the largest family with an estimated 1700 species. This family shows a huge variation in basidioma morphology as well as in ecological strategies, with the most species-rich genera—*Lactarius*, *Lactifluus*, and *Russula*—being mainly agaricoid and ECM. Russulaceae display quite a large number of characters and especially very variable characters that are difficult to determine character states for. Pileus colors, for example, can be very variable within a single species and they form a continuous range of states within and among different *Russula* species. Milkcaps (*Lactarius* and *Lactifluus*) exude a milk-like solution (*latex*), which, however, often changes color after seconds or minutes, or even during drying. The milk might also change the color of the context and the gills. All these characters are generally hard to quantify, but have historically received a lot of attention and importance in the delimitation of species. Also smells and tastes, although sometimes very prominent, are often subjective characters. The same is true for microscopic characters. Basidiospore ornamentation in Russulaceae is a very striking and useful feature but also shows a fairly large amount of intraspecific variation.

Species concepts and species recognition

Species delimitation in Russulaceae followed the morphological species concept until the 1980s and 1990s. A combination of macro- and micromorphological characters was used to delimit and recognize species. Also ecological features such as soil characteristics, vegetation types, and especially host association have always been important in species delimitation of Russulaceae. The biological species concept was never used in this group since it is impossible to bring these ECM fungi in culture, with a few exceptions. As in other groups of Agaricomycota, the onset of molecular tools initially made it clear that some characters, such as fruiting body shape and hymenophore type, had received too much importance in the morphological species concept. From the early 2000s, angiocarpic and sequestrate species were included in the traditional agaricoid genera (Desjardin 2003; Eberhardt and Verbeken 2004; Nuytinck et al. 2004). Molecular tools also made it clear that characters related to the pileipellis structure (both macroscopic and microscopic) have a larger phylogenetical signal than, e.g., ornamentation of basidiospores, pileus pigmentation, and latex (in the case of milkcaps).

Within the milkcaps, striking evolutionary differences are observed between the two genera *Lactifluus* and *Lactarius*. While the high morphological variation in the larger genus *Lactarius* (with about 450 accepted species) is not reflected in its phylogenetic structure with rather short branch lenghts, a large genetic diversity is apparent in the smaller genus *Lactifluus* (with 224 accepted species). This diversity results in very different and distant clades, but also in intricate species complexes, such as the *Lactifluus volemus* complex (De Crop et al. 2021). Van de Putte et al. (2010, 2012, 2016) showed that both morphologically "pseudocryptic" as well as truly cryptic species exist in this complex. Pseudocryptic species look alike at first sight but can be distinguished once appropriate but often subtle characters are considered.

Resupinate Russulales are of high importance in the phylogeny of the group (Larsson and Larsson 2003). Donk (1971) was the first to discuss a possible relationship between taxa such as those mentioned above and other groups possessing a system of gloeoplerous hyphae (gloeocystidia) and amyloid basidiospores. Some examples of phylogenetic studies of species complexes in resupinate Russulales are found in *Aleurodiscus* (Wu et al. 2001; Tian et al. 2018), *Dentipellis* (Zhou and Dai 2013), *Echinodontium* (Liu et al. 2017), *Gloeodontia* (Telleria et al. 2008), and *Heterobasidion* (Dai and Korhonen 2009; Chen et al. 2014).

Regarding the corticioid Russulales, the *Scytinostroma galactinum* complex was biologically considered by Boidin and Lanquetin (1987) and Nakasone and Micales (1988). The species is characterized by the dextrinoid and cyanophilous skeletoid hyphae, presence of gloeocystidia, and narrowly ellipsoid to subcylindrical basidiospores. Boidin and Lanquetin (1987) discussed the separation of four species in the complex based on inter-incompatibility mating tests, also matching with geographical separation (*Scytinostroma galactinum* in North America, *S. neogalactinum* in Central America, *S. africanogalactinum* in tropical Africa, and *S. eurasiaticogalactinum* in Eurasia). Later, Nakasone and Micales (1988) separated the North American relatives in

two inter-incompatible species (*S. galactinum* s.s., typically on gymnosperms, and *S. protrusum* with two subspecies growing on angiosperms and separated by geographic distribution). *Peniophora* species were studied by ITS sequences, mating tests, morphology, and ecological criteria by Hallenberg et al. (1996). In some species regarded as conspecific based on morphological criteria, these authors found intersterility, but such sibling species were not separated by the ITS.

Members of the genus *Hericium* species are coralloid representatives of Russulales. Micromorphological variability can be very subtle among species (Hallenberg et al. 2013); species delimitation has been supported by the evaluation of additional data, including substratum preference, geography, and molecular phylogenetic data. Thus far, only ITS and combined ITS–LSU have been used for species delimitation in *Hericium* (Das et al. 2011, 2013; Hallenberg et al. 2013; Jumbam et al. 2019).

The use of a purely morphological species concept has gradually changed into a preference for using molecular phylogenetic data with morphological support. Relying on DNA alone is rarely done and is recommended against because of richness in morphological features that usually allow for morphology-based species recognition. The most commonly used marker is the ITS barcode, although in some species complexes it is clear that phylogenies based on ITS alone are unresolved. Phylogenies based on multiple unlinked loci provide independent estimates of the organismal phylogeny, and congruence among these estimates furnishes strong evidence of species divergence (Taylor et al. 2000). In Russulaceae, the following markers are often used alongside ITS: LSU, *rpb1*, *rpb2* (De Crop et al. 2014, 2017), *tef1* (De Lange et al. 2021), and more rarely *gpd*, *atp6*, mtSSU, and *Mcm7* (Nuytinck et al. 2007; Van de Putte et al. 2012; Caboň et al. 2017, 2019; Looney et al. 2020).

Conclusion and recommendations

As speciation is an on-going, continuous process, species might have evolved recently and they can suffer from complications such as incomplete lineage sorting. In this case, gene trees may disagree with true species trees and contradict each other. The Bayesian species delimitation technique, which allows to delimit species despite incomplete lineage sorting and thus provides a powerful tool for delimiting species when gene trees are discordant, was applied in Russulaceae by De Crop et al. (2014), Van de Putte et al. (2016), and Looney et al. (2020). Most recent studies combine sequence data from a single or (preferably) different loci with morphological, ecological, and biogeographic characters in an integrative approach.

Species delimitation in Sebacinales

Sebacinales is one of the earliest diverging groups of Agaricomycetes that was separated from Auriculariales based on molecular phylogenetic data (Weiss and Oberwinkler 2001; Weiss et al. 2004). As a heritage from the pre-molecular era, several species of the type genus *Sebacina* still belong to the Auriculariales (e.g., *S. calcea*). Apart from most other agaricomycete orders, Sebacinales is characterized by a few deep lineages and a few dozens of described species. However, Sebacinales display several orders of magnitude greater species-level richness as revealed from molecular studies in soil and plant roots. Sebacinales is divided into two well-delimited families, Sebacinaceae and Serendipitaceae. Serendipitaceae is monogeneric (genus *Serendipita*; Weiss et al. 2016), whereas Sebacinaceae includes eight genera that are well-delimited based on morphological and molecular data (Oberwinkler et al. 2014). Representatives of Sebacinaceae form basidiomata. *Serendipita* species form no basidiomata and their sexual structures are extremely rare (Oberwinkler et al. 2013, 2014).

Sebacinaceae is mainly comprised of ECM symbionts, but the ancestral groups are humus and wood saprotrophs in mostly tropical ecosystems (Oberwinkler et al. 2014). The sebacina lineage is one of the largest groups of ECM fungi, which is relatively common and diverse in all ectomycorrhiza-dominated plant ecosystems from tropical to arctic habitats (Tedersoo et al. 2014b) but only sporadically dominant (Ishida et al. 2007; Mühlmann et al. 2008). Certain taxa in the main clade of *Sebacina* evolved associations with orchids, particularly with species of *Neottia* (Oja et al. 2015; Tesitelova et al. 2015) and *Hexalectis* (Taylor et al. 2003), both of which include non-photosynthetic species that depend entirely on their association with *Sebacina* fungi (McKendrick et al. 2002; Taylor et al. 2003). Both ECM and saprotrophic species form gelatinous, corticioid to clavarioid and auricularioid basidiomata.

Serendipitaceae includes ubiquitous soil saprotrophs that have a strong endophytic affinity to plant roots. For example, *Serendipita* spp. are common in Antarctic soils (Bridge and Newsham 2009) and in roots of various agricultural and grassland plants in Europe (Garnica et al. 2013; Riess et al. 2014). *Serendipita* spp. also colonize thalli of certain hepatics, forming a putatively mutualistic symbiosis (Kottke et al. 2003; Bidartondo and Duckett 2010). Members of *Serendipita* are considered as one of the three main groups of "*Rhizoctonia*" associated with photosynthetic orchids (Warcup and Talbot 1967; Oberwinkler et al. 2013). In particular, *Caladenia* spp. and *Serendipita* spp. are often the only symbionts (Huynh et al. 2009; Wright et al. 2010). Compared with other "*Rhizoctonia*", *Serendipita* spp. are relatively

more common orchid associates in boggy ecosystems (Illyes et al. 2010). Furthermore, certain species of *Serendipita* also establish in ericoid mycorrhizal symbiosis, being one of the most common groups based on molecular surveys in temperate and tropical montane ecosystems (Allen et al. 2003; Selosse et al. 2007). Besides ericoid and orchid mycorrhiza, two small groups of *Serendipita* are ECM with with various tree species (Tedersoo and Smith 2013).

Species concepts and species recognition

Because of high macromorphological plasticity and poor differentiation of micromorphological characters, *Sebacina* comprises a small number of species. However, molecular studies of roots and soil (Tedersoo et al. 2014a, b) suggest the presence of hundreds and perhaps thousands of species. Based on the distribution of ITS sequence similarity among specimens and root tips, Tedersoo et al. (2014b) suggested that $98.0 \pm 0.5\%$ sequence similarity separates the best among molecular species. To our knowledge, ECM Sebacinaceae spp. have remained unculturable. Species of *Serendipita* are relatively difficult to culture, but when successful they are fast-growing. Thus far, cultures are known from the ericoid mycorrhizal and ECM taxa. Species of *Serendipita* (including those described as *Piriformospora*) have been described based on the teleomorph (Warcup and Talbot 1967), the presence or absence and morphology of chlamydospores (Verma et al. 1998) and monilioid cells (Riess et al. 2014), or solely based on differences in the ITS region (Fritsche et al. 2020). Due to the difficulties in culturing and paucity of informative morphological characters, species delimitation in *Serendipita* relies entirely on DNA barcodes. Through clustering optimization, Setaro et al. (2012) determined that a 1% LSU distance threshold corresponds to the 3% ITS threshold in Sebacinales.

Conclusion and recommendations

The paucity of taxonomically informative morphological characters in Sebacinales has led to only a few described species in the order Sebacinales, which contrasts to the two or three orders of magnitude more molecular-based estimated species. It is likely that the species-level taxonomy of Sebacinales continues to utilize arbitrary ITS and LSU sequence similarity thresholds. The lack of cultures in Sebacinaceae and difficulties in obtaining cultures of Serendipitaceae hamper sequencing of protein-coding genes and whole genomes, which is problematic for phylogenetic species recognition. Although closely related species of Sebacinaceae and Serendipitaceae seem to perform similar functions, delimiting species and major strains may be of high importance because of the commercial distribution of certain *Serendipita indica* strains (Oberwinkler et al. 2013) and the obligate dependency of certain orchid species on their *Sebacina* or *Serendipita* symbionts. Fortunately, the ITS region provides sufficient resolution and the LSU provides enough additional information to build phylogenies in both families. One of the outstanding questions is whether species and strains of *Serendipita* are capable of forming both endophytic interactions and mycorrhizal associations with orchids and especially with ericoid plants. From a biotechnology perspective, it is crucial to understand whether commercial inocula are beneficial in various environmental settings and whether they affect local microbial communities. Finally, for the sake of good taxonomic practices, "*Sebacina*" species belonging to Auriculariales should be formally transferred.

Species delimitation in Trechisporales

A small order with about 120 known species in 16 genera (He et al. 2019), Trechisporales comprises mostly corticioid (=crust-like) fungi, some of which have a poroid hymenophore. Members of the order are morphologically diverse—some genera as *Luellia*, *Subulicystidium*, and *Tubulicium* were recovered in the order only because of molecular phylogenetic analyses since they have no morphological traits in common with *Trechispora*, the type genus. All species have a monomitic hyphal system with clamped hyphae and many species have rhizomorphs. The nutritional mode is not known but species often occur on strongly decayed wood or other debris on the ground and there is the possibility that at least some species are soil-dwelling saprotrophs or involved in interactions with plants (Larsson 2007; Dunham et al. 2007).

Species concepts and species recognition

Species in *Trechispora* exhibit a wide range of hymenophore configurations with smooth as well as hydnoid and poroid representatives. The variable macromorphology contrasts with a strikingly uniform micromorphology with a combination of characteristics that make the genus well defined. Some of these features are a fragile context, presence of cords, ampullately widened septa in cords and subiculum, short-celled, richly branching subhymenial hyphae, and small, usually ornamented basidiospores with a rounded to ellipsoid outline (Larsson 1996). One remarkable character is the ampullate septa, present on subicular hyphae and especially on some hyphae of the mycelial cords. Calcium oxalate crystals often adhere to the subicular hyphae, the morphology of which can be useful for species identification (Larsson 1994). There are some problems to delimit siblings among some *Trechispora* species. For example, *T. farinacea* is a variable species, even in the more restricted sense (Larsson 1995, 1996) it is still variable and may contain multiple

species. *Trechispora farinacea* s.s. has not been reported outside northern temperate areas, and biogeography may currently be the best way to separate it from similar tropical or subtropical relatives (Chikowski et al. 2020). *Brevicellicium* has investigated based on molecular data by Telleria et al. (2013). It is characterized by a corticioid habit, isodiametric subhymenial hyphae, short basidia, and smooth, often subangular basidiospores with a distinct apiculus. It was phylogenetically recovered close to other *Trechispora* species. Another genus of corticioid fungi recently considered by molecular phylogeny is *Subulicystidium*, members of which are characterized by the subulate cystidia encrusted with rectangular crystals, and usually vermiform basidiospores. Usually, species in *Subulicystidium* have been delimited exclusively based on the size and shape of basidiospores. With the use of ITS and LSU, Ordynets et al. (2018, 2020) demonstrated a rather broad intraspecific variation in *Subulicystidium* species.

Conclusion and recommendations

As suggested by Chikowski et al. (2020), the ITS region is strongly variable within *Trechispora* and serves well as a species delimitation barcode. However, for phylogenetic approaches, it is too variable and sequences from alternative markers must be incorporated in multilocus reconstructions to elucidate the relationships among species of *Trechispora* and *Scytinopogon*. It is expected that many undiscovered species of Trechisporales reside in tropical and subtropical areas and the collecting efforts may consider these working areas (see, e.g., the recently described *Trechispora hondurensis*; Haelewaters et al. 2020a). Usually is very difficult to get DNA from most of the species because of the thin basidiomata and pure cultures are often difficult to obtain. The use of morphological features alone is insufficient to discriminate closely related species. More sequences, including from material from tropical areas, are required to construct a robust modern phylogeny of Trechisporales and to provide a good idea about species relationships.

Notes

We were unable to compile detailed information for the orders Auriculariales, Cantharellales, Hysterangiales, Phallales, and Thelephorales. We refer to the following state-of-the-art papers. For Auriculariales: Yan et al. (1999, 2002), Montoya-Alvarez et al. (2011), Looney et al. (2013), and Spirin et al. (2019). For Cantharellales: Olariaga et al. (2009, 2017) and Buyck and Hofstetter (2011). For Hysterangiales: Elliott et al. (2020). For Phallales: Cabral et al. (2019) and Melanda et al. (2020). For Thelephorales: Ramírez-López et al. (2015), Vizzini et al. (2016a), Svantesson et al. (2019), and Nitare et al. (2021). In general, these orders follow the pattern that has emerged for other orders within Agaricomycetes; an integrated or polyphasic approach is encouraged to successfully delimit taxa. In addition, increased sampling is needed from understudied areas of the world (e.g., Vizzini et al. 2016a, b; Cabral et al. 2019; Cheek et al. 2020).

Species delimitation in Bartheletiomycetes

Bartheletiomycetes is a monotypic class within Basidiomycota, and probably the earliest-diverging class of Agaricomycotina (Mishra et al. 2018). The only species in the class, *Bartheletia paradoxa*, is characterized by a unique mixture of characteristics, some of which bear resemblance to the other two major groups of the Basidiomycota, Pucciniomycotina and Ustilaginomycotina (Scheuer et al. 2008). *Bartheletia paradoxa* grows on fallen leaves of a single species, *Ginkgo biloba*, throughout the winter. If the fungus is also present as an endophyte is currently unclear, even though anecdotal observations support this idea (Mishra et al. 2018). On the fallen leaves, sori of 0.1–2.0 mm develop in autumn, which produce a slimy mass of cream-colored yeasts similar in appearance to yeasts of smut fungi. After some time, production of yeasts ends and dark brown to black teliospores develop in the sori, reminiscent of teliospores in Pucciniomycotina. These teliospores oversummer and germinate in autumn to produce longitudinally septate phragmobasidia similar to other members of early-diverging Agaricomycotina (Scheuer et al. 2008). *Bartheletia paradoxa* is considered a "living fossil" and no close phylogenetic relatives are known.

Species concepts and species recognition

As *Bartheletia paradoxa* is the sole species in the class and can be easily recognized by the symptoms it causes on fallen leaves of its hosts, identification based macroscopic observation is possible. The sexual cycle apparently depends on infestation of the correct host (Scheuer et al. 2008); the fungus can only be found on *Ginkgo biloba* leaves. This is an interesting observation because *Ginkgo* has a long history of cultivation and use as an ornamental tree around the world (Arnaud 1954; Kirschner and Okuda 2013).

Conclusion and recommendations

Bartheletia paradoxa has been a taxon of unclear affinity until phylogenomics revealed its isolated position (Mishra et al. 2018). Its recognition at class-level has thus far not been contested and is included at that rank in the latest *Outline of* Fungi *and fungus-like organisms* (Wijayawardene et al. 2020). Even though currently only a single species of Bartheletiomycetes is known, it is recommended that, if

only the yeast stage is visible on the *Ginkgo biloba* leaves, microscopy be done to ensure the presence of long and thin yeast cells, as other basidiomycetous yeasts may also form colonies on the leaves.

Species delimitation in Dacrymycetes

Dacrymycetes is a relatively small class within Basidiomycota, characterized by the earliest emergent type of brown wood rot (Floudas et al. 2015; Nagy et al. 2016). Most members develop gelatinous yellow-shaded basidiomata pigmented with carotenoids. The basidiomata are of pustulate-pulvinate, cupulate, dendroid, and spathulate shapes, except for *Dacryonaema rufum* with its synnematous basidiomata and members of the genus *Cerinomyces*, which are recognized by a corticioid morphotype and arid or firm-gelatinous consistency. Microscopically, Y-shaped bisterigmate basidia effectively separate Dacrymycetes from other Basidiomycota. *Unilacryma unispora* is the only outlier; it develops unisterigmate basidia but otherwise features typical dacrymycetous morphology. The class comprises two orders (Dacrymycetales and Unilacrymales), four families (Cerinomycetaceae, Dacrymycetaceae, Dacryonaemataceae, Unilacrymaceae), 14 accepted genera (*Arrhytidia*, *Calocera*, *Cerinomyces*, *Cerinosterus*, *Dacrymyces*, *Dacryomitra*, *Dacryonaema*, *Dacryopinax*, *Dacryoscyphus*, *Ditiola*, *Femsjonia*, *Guepiniopsis*, *Heterotextus*, *Unilacryma*), and at least 120 species, connected to some of the ca. 400 species names published so far (Shirouzu et al. 2009; Oberwinkler 2014; Savchenko unpubl. data). In the class, generic definitions are historically based on macromorphological characters, such as shape and color of basidiomata. However, phylogenies have showed homoplasy of many traits used in genus delimitation (Shirouzu et al. 2013; Zamora and Ekman 2020). For example, species with *Calocera*-like cylindrical basidiomata are scattered over Dacrymycetaceae and occur at least six non-sister clades (Shirouzu et al. 2017). Nevertheless, many species can be reliably identified with combined morphological and DNA data—even though generic destinations remain rather arbitrary.

Species concepts and species recognition

Species delimitation in the class center on a well-established set of morphological criteria. Macroscopic characters include shape and color of basidiomata, presence of a stalk, orientation of hymenium, and degree of gelatinization. Microscopic features include but are not limited to the presence and shape of clamp connections; wall thickness of subicular, subhymenial, and terminal hyphae; presence of sterile elements in hymenium (=hyphidia, traditionally called dikaryophyses); type of basidia; shape and septation of basidiospores; and presence and shape of conidia. Currently, new species are rarely proposed in Dacrymycetes without support of DNA sequences. The most commonly employed DNA markers are the ITS and LSU (e.g., Kirschner and Yang 2005; Shirouzu et al. 2009, 2017). The least variable rDNA regions, SSU and LSU, sometimes lack barcode qualities, but are widely used in phylogenies because they are easier to align compared to the ITS1 and ITS2 spacer regions. Protein-coding genes such as *rpb1*, *rpb2*, and *tef1* provide high resolution at species level, and also align well over distant taxonomic groups of the class, however, they are scarce in public sequence databases. Mitochondrial genes have only seldomly been used for species delimitation, but preliminary results are promising (Zamora and Ekman 2020).

Other features used for species delimitation are substrate preferences and geographic distribution. Whereas associations with certain species of woody plants are not confirmed in Dacrymycetes, occurrence on coniferous and/or deciduous wood is often a stable character. Preferences for condition or fraction of wood seems to be of importance but cannot be verified with the thus far available data. Knowledge on geographic distribution facilitates identification—there are only few examples left of cosmopolitan species (e.g., *Calocera viscosa*, *Dacryopinax spathularia*). Other methods such as electron microscopy of hyphal septa, karyotic studies, and mating experiments are applied to Dacrymycetes but rarely extended to species-level taxonomy. For example, the number of nuclei in young basidiospores was shown to separate Cerinomycetaceae from the rest of the families (two vs. one nucleus), but this character does not distinguish any lower ranks (Zamora and Ekman 2020).

Conclusion and recommendations

Even though the character framework for polyphasic species delimitation is stable over the class, weight of the same traits may vary among groups, especially in aspects of morphology. Generally, species with larger structures are allowed to have wider trait distributions (e.g., *Femsjonia* and related taxa), and species with smaller structures are defined by more conservative ranges (e.g., *Cerinomyces*). Potential conflicts between broad and narrow concepts can arise in groups with simple but highly variable morphologies, such as clamp-less members of *Dacrymyces* with three-septate basidiospores. Simultaneously, the order demonstrates high intragenomic polymorphism of the ITS region (Savchenko unpubl. data). Thus, over-reliance on a certain cutoff threshold in ITS sequences can overestimate species richness. Such difficult cases are mostly unresolved and will require careful analyses and deliberated taxonomic decisions. True cryptic taxa are rare in the class; most species can be unambiguously identified by a combination of characters. Examination of multiple fresh samples, emphasis on microscopic characters,

and sequencing and analysis of multiple loci help to define accurate species limits. Dacrymycetes can be rare in nature, and descriptions based on a single specimen are often unavoidable. In these cases, researchers must refer to existing literature and unsequenced taxa as to make sure that characteristics of a newly proposed taxon do not overlap with previously described species.

Species delimitation in Tremellomycetes

Tremellomycetes (Agaricomycotina, Basidiomycota) includes more than 350 species in 71 genera (Wijayawardene et al. 2020) and encompasses a variety of fungi both in morphology and lifestyle. The class includes anamorphic yeasts and dimorphic species that form hyphae or conspicuous macroscopic basidiomata (Hibbett et al. 2007; Boekhout et al. 2011; Liu et al. 2015a). Tremellomycetous fungi are ecologically heterogeneous, comprising saprotrophs, mycoparasites, human pathogens, and lichenicolous fungi (Diederich 1996; Boekhout et al. 2011; Millanes et al. 2011; Weiss et al. 2014).

Species concepts and species recognition

Tremellomycetous species were conventionally identified based on morphological features and other phenotypic characters, such as chemotaxonomic criteria and physiological properties (Bauer et al. 2006; Celio et al. 2006; Kurtzman et al. 2011). However, these methods proved insufficient to distinguish tremellomycetous species; the morphological species concept is not good for this group for the following reasons. Tremellomycetes contains a large number of unicellular yeast taxa that have fewer morphological characters. Furthermore, the microscopic fungi with fewer cells, such as yeasts, may have a slower rate of morphological change over time (Taylor et al. 2006a, b). Genetic isolation can be detected ahead of recognizable morphological change; tremellomycetous taxa with similar morphological characters often present nucleotide variation and comprise more than one (phylogenetic) species (Scorzetti et al. 2002; Yurkov et al. 2015a). A portion of dimorphic fungi in Tremellomycetes often produce macroscopic basidiomata. Before the One Fungus One Name (1F1N) principle (Hawksworth et al. 2011; Wingfield et al. 2012), the teleomorphic and anamorphic states used to be identified and named separately based on their different morphology. Therefore, one species may have two different names based on morphology. Tests with mating compatible individuals are the key evidence to identify biological species (Boekhout et al. 2021). However, the vast majority of tremellomycetous fungi are anamorphic taxa that lack a sexual stage (Liu et al. 2015a). For the teleomorphic, basidioma-forming fungi, the sexual stage might be difficult to cultivate in the lab. Basidiospores, however, can be cultured for some genera (Liu et al. 2015a). Though biological species recognition has been applied to Tremellomycetes (Boekhout et al. 2021), this approach is impractical for many taxa in the class.

Phylogenetic species recognition has been extensively used and an increasing number of new species have been introduced in Tremellomycetes using phylogenetic data. The D1/D2 domains of the LSU was initially examined and found to resolve closely related species for yeast species (Peterson and Kurtzman 1991). The LSU has been used as a stable marker for yeast species identification (Fell et al. 2000). The ITS is often used to resolve species in conjunction with the LSU D1/D2 domains (Scorzetti et al. 2002). A comprehensive sequence database of these two genes for almost all known basidiomycetous yeast species has been developed (https://theyeasts.org/). It is feasible to rapidly delimit tremellomycetous fungi species based on this platform. However, not all clades tested are strongly supported in rDNA trees, and protein-coding genes including *rpb1*, *rpb2*, and *tef1* are often applied. The combination of rDNA with protein-coding genes exhibits the strongest support and best resolution for species delimitation of Tremellomycetes fungi (Liu et al. 2015b).

Not all species defined by phylogenetic analyses in Tremellomycetes have distinctive phenotypic characteristics when compared with sibling species. Ecology and environment preference should be considered as well to understand species limits. Species in the genus *Goffeauzyma* do not possess unique morphological or phenotypic characters, however, they can be seen as an ecoclade—species of this genus are limited to an acid aquatic environment (Gadanho and Sampaio 2009; Russo et al. 2010). Host specificity also can be considered in species delimitation when researching mycoparasitic taxa (Millanes et al. 2014), such as *Tremella* s.l. (Chen 1998).

Conclusion and recommendations

Not a single method can delimit tremellomycetous species thoroughly alone. It is recommended to use molecular phylogenetic data, morphological characters, chemotaxonomic and physiological properties, ecological information, and host specificity data as integrated criteria for Tremellomycetes. For phylogenetic analyses, the LSU D1/D2 domains serves as the barcode marker for yeasts, and should be combined with ITS and protein-coding genes (*rpb1*, *rpb2*, *tef1*) for accurate species delimitation in the class.

Species delimitation in Wallemiomycetes

The genus *Wallemia*, with type species *W. ichthyophaga*, was described by Johan-Olsen (1887) from salted fish. Almost a century later, von Arx (1970) synonimized the genus *Sporendonema* with *Wallemia* and introduced a new combination, *W. sebi*, for the species *Sporendonema sebi*. Zalar et al. (2005) performed a first molecular phylogenetic study on *Wallemia*, based on SSU and ITS rDNA. In accordance to the concept of polyphasic taxonomy, based on the phylogenetic reconstruction of an ITS dataset and phenotypic characters (xerotolerance, morphology), *W. ichthyophaga* and *W. sebi* were recognized and *W. muriae* was proposed as a new combination for *Torula epizoa* var. *muriae* (Zalar et al. 2005). The genus currently contains eight species: *W. ichthyophaga*, *W. muriae*, *W. sebi* (Zalar et al. 2005), *W. canadensis*, *W. mellicola*, *W. tropicalis* (Jančič et al. 2015), *W. hederae* (Jancic et al. 2016a), and *W. peruviensis* (Díaz-Valderrama et al. 2017). *Wallemia* species are found in ecological niches with reduced water activity. They have been isolated from solar salterns; low-water activity (a_w) products such as high sugar and salt content foods; dust, urban, and indoor air; and agricultural environments (Zajc et al. 2011; Jančič et al. 2016b).

For nearly 100 years, the genus *Wallemia* had a special status in mycology. It was Terracina (1974) who introduced it in Basidiomycota, primarily based on structures that resembled dolipores. Their uniqueness was the primary reason for the description of a new family Wallemiaceae, accommodating the genus *Wallemia*. Wallemiaceae was first placed in the order Filobasidiales (Moore 1996). Due to its unique phylogenetic position at the base of the Basidiomycota phylogenetic tree, in combination with its morphology and xerotolerance, it was placed into newly described order Wallemiales and new class Wallemiomycetes (Zalar et al. 2005). Analyses of rDNA loci (SSU, ITS, LSU) and three protein-coding genes (*rpb1*, *rpb2*, *tef1*) reinforced the isolated position of the class Wallemiomycetes in Basidiomycota (Matheny et al. 2007). The class was assigned to Basidiomycota *incertae sedis*, reflecting ambiguity about its higher-level placement (Zalar et al. 2005; Matheny et al. 2007). While a comparative phylogenomic analysis, based on 14 fungal proteomes, indicated that Wallemiomycetes is a 250 million-year-old sister group to Agaricomycotina (Zajc et al. 2013), the phylogenetic reconstruction of a six-locus dataset (SSU, 5.8S, LSU, *tef1*, *rpb1*, *rpb2*) and a tree produced from amino acid data extracted from published genomes (115 taxa, 396 proteins) placed Wallemiomycetes in subphylum Wallemiomycotina (Zhao et al. 2017). Mishra et al. (2018), however, were unable to resolve whether *Barthelia* or *Wallemia* is the first-diverging lineage in Agaricomycotina—this study was also based on the analyses of genome sequences. In the genome-scale phylogeny of Fungi by Li et al. (2021), Wallemiomycotina was retrieved as sister to Agaricomycotina with strong support but *Barthelia* was not included in this analysis. Given the unresolved position of *Barthelia* + *Wallemia* at the base of Agaricomycotina, we follow a conservative approach and treat Wallemiomycetes as part of Agaricomycotina.

Species concepts and species recognition

Fungi of the genus *Wallemia* grow on solid media as small and very dusty colonies, due to the huge production of conidia (Zalar et al. 2005). Thus far, only production of asexual spores has been described (Padamsee et al. 2012). *Wallemia* displays a special form of conidiogenesis. It forms chains of blastic conidia. The fertile hypha becomes septated and separates into four cylindrical cells, which swell and disassemble. Although the sexual morphotype was not discovered yet, genomic analyses of *W. ichthyophaga*, *W. mellicola*, and *W. sebi* have identified genes related to sexual reproduction (Padamsee et al. 2012; Zajc et al. 2013; Gostinčar et al. 2019; Sun et al. 2019).

The most informative loci for delimiting *Wallemia* species outside of the *W. sebi* complex are the SSU and ITS regions (Zalar et al. 2005; Jančič et al. 2015, 2016a, b). Within the *W. sebi* complex, species can be distinguished by addional loci, including *Mcm7*, *rpb1*, *rpb2*, pre-rRNA processing protein (*Tsr1*), and 3-phosphoadenosine-5-phosphatase (*Hal2*) (Jančič et al. 2015). Beside notable differences in DNA sequences, species of *Wallemia* are distinguished by conidial size, xerotolerance, halotolerance, chaotolerance, growth temperature regimes, extracellular enzyme activity profiles, and secondary metabolite patterns.

Conclusion and recommendations

Phylogenetic and phylogenomic studies support separation of species complexes into separate taxa. Species delimitation in *Wallemia* can be supported by growth on media with lowered a_w—as one of the most xerophilic taxa in the entire fungal kingdom (Zajc et al. 2014a, 2014b). Species in Wallemiomycetes are delimited based on differences in conidial size, tolerance to low a_w (xerotolerance), tolerance to NaCl (halotolerance), tolerance to $MgCl_2$ (chaotolerance), growth temperature range, physiological characteristics, and secondary metabolites (Jančič et al. 2015, 2016a).

Subphylum Pucciniomycotina

Species delimitation in Agaricostilbomycetes

Agaricostilbomycetes currently comprises one accepted order (Agaricostilbales), five families (Agaricostilbaceae, Chionosphaeracea, Jianyuniaceae, Kondoaceae, Ruineniaceae), and at least 74 accepted species in 13 genera (Aime et al. 2014; Begerow et al. 2018; He et al. 2019; Li et al. 2021). Members of Agaricostilomycetes are morphologically and ecologically diverse. Different phylogenetic studies have recovered long branches in Agaricostilbomycetes, probably reflecting the high degree of heterogeneity and thus far undiscovered diversity (Weiss et al. 2004; Bauer et al. 2006; Wang et al., 2015b).

Agaricostilbomycetes comprises teleomorphic, dimorphic, and anamorphic fungi, of which the latter are known only from an asexual yeast stage. Basidiomata are generally minute, ranging from stilboid (e.g., *Chionosphaera*, *Sterigmatomyces*, and *Stilbum*) to pustulate (e.g., *Mycogloea nipponica*) (Oberwinkler and Bandoni 1982a; Bandoni 1998). In general, teleomorphic taxa in Agaricostilbomycetes are characterized by statismosporic, transversally septate basidia. Remarkable exceptions are the holobasidiate species of *Chionosphaera* (Kirschner et al. 2001b) and the ballistosporic basidia of *Kondoa* spp. (only observed in culture). *Mycogloea nipponica* possesses basidia that become finally detached from their probasidia (Bandoni 1998; Kirschner et al. 2003).

Species of Agaricostilbomycetes have been isolated from various substrates and habitats: *Agaricostilbum* spp. from palm litter; *Mycogloea nipponica* in association with ascomycetous hosts on wood; *Chionosphaera cuniculicola* from bark beetle galleries in *Picea* logs; *Cystobasidiopsis nirenbergiae* from soil; and *Bensingtonia*, *Kondoa*, and *Myxariophila* spp. from basidiomata of other fungi (Oberwinkler and Bandoni 1982a; Bandoni 1998; Kirschner et al. 2001b; Bauer et al. 2009; Li et al. 2021). Many species are assumed to be mycoparasitic, although the interaction mechanisms between parasite and host remain unclear (Wang et al. 2015c; Oberwinkler 2017; Begerow et al. 2018).

Species concepts and species recognition

For teleomorphic and dimorphic taxa in Agaricostilbomycetes, most species were traditionally described and delimited following the morphological species concept. Macro- and micromorphological characters were used, such as basidioma shape and texture, shape and dimensions of basidia, basidiospores, hyphae, and eventually other cells (e.g., conidia, haustoria). Sometimes, ultrastructural observations, culture characteristics, and ecological information were incorporated in species descriptions. Since the 2000s, sequence data are incorporated in species delimitation studies, in particular markers of the rDNA operon (Kirschner et al. 2001b, 2003; Bauer et al. 2009). Some of the teleomorphic species have been grown in culture, leading to new insights. For example, Kirschner et al. (2003) found that *Mycogloea nipponica* is the sexual stage of a representative in the yeast-genus *Kurtzmanomyces*.

Species delineation of yeast taxa comprises culture characteristics such as colony morphology, micromorphology, type of division, and physiological characteristics. Currently, sequence data have become an important tool for species identification and delimitation. The work of Wang et al. (2015b, c) introduced an excellent seven-locus (SSU, ITS, LSU, *rpb1*, *rpb2*, *tef1*, *cytb*) reference dataset for most basidiomycetous yeasts, which has been used to delineate new species and higher taxa in Agaricostilbomycetes. Most recently, Li et al. (2021) described 18 new species, three new genera, and one new family in Agaricostilbomycetes, based on the phylogenetic reconstruction of a seven-locus dataset as well as an LSU D1/D2 dataset, completed with physiological profiles and morphological characterizations of all newly described species.

Conclusion and recommendations

Since Agaricostilbomycetes contain yeasts, filamentous fungi, and dimorphic fungi, different methodologies and species concepts have been established for species delimitation. Delimitation of yeast species involves physiological profiles and biochemical characters, complemented with molecular phylogenetic reconstructions of multilocus datasets (ranging from the LSU D1/D2 up to seven loci). Species delimitation of filamentous taxa involves morphological analyses of macro- and microcharacters, completed with phylogenetic analyses of ITS–LSU datasets. The seven-locus dataset from Wang et al. (2015b, c) may be used as reference dataset for new taxon discovery and species delimitation in the group. However, it is important to work integratively, also studying and comparing more traditional characters of teleomorphic and anamorphic fungi among different taxa. A challenge in the description of teleomorphic taxa is to obtain an eventual asexual yeast stage, and to integrate characters from sexual and asexual stages. Similarly, it is important to study the formation of sexual structures in yeasts (Kirschner et al. 2003).

Species delimitation in Atractiellomycetes

Atractiellomycetes is a heterogenous group of fungi (Aime et al. 2018b) characterized by a synapomorphy at the ultrastructural level: the symplechosomes. These structures are stacked plate-like cisternae, interconnected by hexagonally arranged filaments and sometimes connected to

mitochondria (Bauer and Oberwinkler 1991b; McLaughlin et al. 2017). However, their function is unknown and only few species have been investigated for their ultrastructural anatomy. Atractiellomycetes contains one order (Atractiellales), three families (Atractogloeaceae, Hoehnelomycetaceae, and Phleogenaceae), ten genera (*Atractidochium*, *Atractogloea*, *Basidiopycnis*, *Bourdotigloea*, *Helicogloea*, *Hobsonia*, *Phleogena*, *Proceropycnis*, *Saccosoma*), and at least 58 species (Aime et al. 2018b; Begerow et al. 2018).

Basidiomata of Atractiellomycetes range from corticioid over stilboid to pycnidioid. Basidia are typically transversally septate; with or without laterally attached saccate probasidium; and with ballistospores, or statismospores in *Atractogloea* and *Phleogena* (Oberwinkler and Bandoni 1982b). Some *Helicogloea* species have an asexual morph, formerly classified as *Infundibura*, *Leucogloea*, and *Pleurocolla* (Kirschner 2004), whereas few other Atractiellomycetes are known from asexual stages only, e.g., *Proceropycnis pinicola* (Oberwinkler et al. 2006). The anamorphs of species are sporodochial or pycnidial; members of this class do not produce yeasts (Aime et al. 2014; Oberwinkler 2017).

The ecological niches of Atractiellomycetes species are heterogenous, and hint at a possibly large, yet undiscovered diversity. Species of *Bourdotigloea*, *Helicogloea*, and *Saccosoma* are presumed saprotrophs on plant material, and some have been reported to grow on or in hymenia of other fungi; *Atractidochium hillariae* was isolated as an endophyte of *Pinus taeda* needles; *Atractiella rhizophila* and *Proceropycnis hameedii* were isolated as *Populus* root endophytes; *Basidiopycnis hyalina* and *Proceropycnis pinicola* were isolated from conifer samples infested with bark beetles; *Phleogena faginea*, an enigmatic stilboid fungus with statismospores, grows on decaying trunks and branches of various deciduous tree species (Oberwinkler et al. 2006; Bonito et al. 2017; Aime et al. 2018b; Spirin et al. 2019).

Species concepts and species recognition

Since Atractiellomycetes comprises filamentous species only, species delimitation has traditionally been based on macro- and micromorphological analyses of basidiomata and microscopic structures. The largest group in this class are the resupinate corticioid species, characterized by laterally attached saccate probasidia (Baker 1936). Species with these characters were originally referred to two genera *Helicogloea* and *Saccoblastia*. Subsequent species from various regions of the world were delimited mainly based on micromorphologcal analyses, including the shape and dimensions of hyphae, basidia, basidiospores, and cystidia when present (Baker 1936, 1946; Wells 1990; Chen and Oberwinkler 2000; Kirschner 2004; Schoutteten et al. 2018).

Due to a lack of sequence data of resupinate Atractiellomycetes, a first taxonomic treatment supported by molecular phylogeny was only published recently. Spirin et al. (2019) generated ITS and LSU sequences for many representatives of the resupinate Atractiellomycetes. Three genera were clearly delimited, supported by both molecular and morphological evidence (*Bourdotigloea*, *Helicogloea*, *Saccosoma*). The traditionally used morphological characters were generally consolidated as good characteristics; in most cases, species can be identified by careful measurements of hyphae, basidia, and basidiospores. Other data such as geography and substrate seem to be good characters to distinguish species in some cases, although the current dataset is too limited to make sound conclusions (Spirin et al. 2019; Malysheva et al. 2020). Most difficulties reside in the genus *Bourdotigloea*, where interspecific variability in rDNA sequences is limited (Spirin et al. 2019). Although species in this group are capable of growing in axenic culture (Schoutteten unpubl. data), only very few of them have been isolated in pure culture and physiologically characterized.

Several species from other genera of Atractiellomycetes have been described from cultures. These representatives are generally found on long branches in phylogenetic reconstructions and have been isolated from various substrates. Sequence data for these representatives are generally limited to the rDNA loci (Oberwinkler et al. 2006; Bonito et al. 2017; Aime et al. 2018b).

Conclusion and recommendations

The best studied lineage of Atractiellomycetes are the resupinate taxa. Species delimitation has recently moved from a morphological concept to an integrative approach, incorporating morphology, phylogenetic reconstructions based on ITS and LSU, biogeography, and substrate. This lineage has been well-sampled in northern and western Europe, although these species occur in most parts of the world and much diversity remains to be discovered. Recent studies show that intraspecific morphological variability may be large (e.g., in *Helicogloea sebacea*; Malysheva et al. 2020). Further sampling is needed to further test the set of characters currently used for species delimitation. Sequencing of more nuclear markers—including protein-coding genes—may prove helpful for species delimitation in challenging genera such as *Bourdotigloea*.

Species delimitation in Classiculomycetes

The class Classiculomycetes was erected by Bauer et al. (2006) to accommodate two species of aquatic mycoparasites: *Classicula fluitans* and the anamorphic *Jaculispora submersa*. Qiao et al. (2018) recently described a second species of *Classicula* from China. All species are characterized by navicular conidia, a character shared with many

aquatic hyphomycetes. Classiculomycetes currently contains one order (Classiculales), one family (Classiculaceae), two genera (*Classicula*, *Jaculispora*) and three species (Begerow et al. 2018; He et al. 2019).

Species concepts and species recognition

The species concept used in this class integrates micromorphological characters with molecular phylogenetic inferences, based on rDNA. *Classicula fluitans* was originally described as an anamorphic filamentous fungus (*Naiadella fluitans*) isolated from leaf litter in a stream in Canada (Marvanová and Bandoni 1987; Bauer et al. 2003). This fungus is characterized by clamped hyphae, tremelloid haustorial cells, and binucleate navicular conidia. Qiao et al. (2018) described *C. sinensis* from leaf litter in China. Following isolation in pure culture, the micromorphology of *C. sinensis* was compared with *C. fluitans*, supported by molecular phylogenetic reconstruction. Regrettably, *C. sinensis* is only illustrated by a few pictures; neither detailed drawings nor ultrastructural observations were presented.

Conclusion and recommendations

Only few studies in this class have been published. Recent studies combine detailed micromorphological observations with phylogenetic reconstructions of rDNA datasets for species delimitations (Bauer et al. 2003; Qiao et al. 2018). Currently, our knowledge on the diversity of this class is limited to three species. The real species diversity may be much larger, especially given that freshwater ecosystems are a traditionally undersampled niche for fungi. Since these fungi have few morphological characters available for species delimitation, it is important to perform detailed study of microscopic structures and to generate high-quality sequence data. The current understanding is that conidiogenesis and conidia are important characters for species delimitation. Basidia and basidiospores are important for delimitation in various fungal genera, which may be also true in this group. Efforts should be made to induce the formation of these structures in pure culture, as outlined in Bauer et al. (2003). Isolation of these fungi in culture also allows to generate sequence data. To date, most reference data are nuclear rDNA sequences. Future analyses incorporating the seven loci used by Wang et al. (2015b, c) may render more stable phylogenetic trees and improved support for species delimitation.

Species delimitation in Cryptomycocolacomycetes

Cryptomycocolacomycetes contains one order (Cryptomycocolacales), one familly (Cryptomycocolaceae), and two monotypic genera (*Colacosiphon*, *Cryptomycocolax*) (Begerow et al. 2018; He et al. 2019). The class was erected by Bauer et al. (2006) to accommodate two genera of mycoparasites that interact with their hosts through colacosomes (Oberwinkler and Bauer 1990; Kirschner et al. 2001a). The phylogenetic clustering of *Colacosiphon filiformis* and *Cryptomycocolax abnormis* is also supported by morphology and ultrastructural characters. Reproductive organs are rather atypical compared to other Basidiomycota. The sporogenous cells are long, aseptate or septate, and giving rise to a various number of sessile spores. In *Cryptomycocolax*, meiosis has been observed in the sporogenous cells, which were consequently interpreted as basidia. The sporogenous cells in *Colacosiphon* are of dubious nature and have been tentatively interpreted as conidiophores. At the ultrastructural level, the septal pores are surrounded by Woronin body-like microbodies. Two types of colacosomes have been observed in the class (Bauer 2004). Thus far, only partial LSU sequences are available for these species—impeding a stable molecular-based classification for the class.

Species concepts and species recognition

Cryptomycocolax abnormis was described as a slimy layer growing on small ascomata on decaying *Cirsium* plant remnants (Asterales, Asteraceae) in Costa Rica. *Colacosiphon filiformis* was found in co-culture with an ascomycetous host derived from bark beetle galleries in *Pinus sylvestris* (Pinales, Pinaceae) in Germany. Both species differ in the production of basidiomata, presence or absence of clamps, reproductive organs, and the types of colacosomes. Description and delimitation of species require detailed macro- and micromorphological observations, including ultrastructural details. Co-cultivation of host and mycoparasite may be helpful for these observations and to obtain enough material for molecular work.

Conclusion and recommendations

Cryptomycocolacomycetes contains only two representatives, but they show a significant amount of variation in morphology, ultrastructure, and ecology. A large phylogenetic distance is observed between these species—although this was just based on partial LSU (Bauer et al. 2006). Comparison of homologous reproductive organs is often used for species delimitation in Basidiomycota, although it is not always easy or possible to interpret the sexual or asexual nature of these structures, especially in this class. The true diversity within the class is likely much larger than currently known. The description and delimitation of new taxa involve detailed observations of macro- and micromorphological characters and investigation of ultrastructural characters, either based on basidiomata or (co-)cultivation assays. Caution is in order when interpreting reproductive organs, as

basidia may be of deviating shape compared to other Basidiomycota, and confusion with asexual structures might be possible. Efforts should be made to sequence multiple markers for phylogenetic-based species delimitation.

Species delimitation in Cystobasidiomycetes

The class Cystobasidiomycetes was erected by Bauer et al. (2006) to accommodate yeast species and a few dimorphic fungi, mostly presumed mycoparasites. The class contains three orders (Cystobasidiales, Erythrobasidiales, Naohideales), eight families (Buckleyzymaceae, Cyphobasidiaceae, Cystobasidiaceae, Erythrobasidiaceae, Microsporomycetaceae, Naohideaceae, Sakaguchiaceae, Symmetrosporaceae), fifteen genera (*Bannoa*, *Begerowomyces*, *Buckleyzyma*, *Cyphobasidium*, *Cyrenella*, *Cystobasidium*, *Erythrobasidium*, *Halobasidium*, *Hasegawazyma*, *Naohidea*, *Microsporomyces*, *Occultifur*, *Robertozyma*, *Sakaguchia*, *Symmetrospora*), and at least 53 species (Wang et al. 2015c; Yurkov et al. 2015b; Begerow et al. 2018; He et al. 2019; Li et al. 2021). A synapomorphic feature of Cystobasidiomycetes taxa is the lack of fucose in the cell wall carbohydrates. Dimorphic genera include *Bannoa*, *Cystobasidium*, *Naohidea*, *Occultifur*, and *Sakaguchia*. Some filamentous taxa are assigned to the genus *Cystobasidium* based on morphological features—thick-walled probasidia, giving rise to thin-walled transversely septate basidia—but no efforts have been made to isolate these species in pure culture (e.g., Martin 1939; Olive 1952). *Bannoa* and *Erythrobasidium* produce holobasidia, whereas other dimorphic species have transversally septate basidia. Mycoparasitic interactions of *Cystobasidium*, *Naohidea*, and *Occultifur* are enabled by tremelloid haustoria forming nanopores at the contact surface. Cystobasidiomycetes representatives have been isolated from various habitats, including other fungi, lichens, phylloplanes (leaf surfaces), bronchial tissues, beetle guts, soil, freshwater habitats, marine habitats, sea sponges, and air (Olive 1952; Oberwinkler 1990; Wang et al. 2015b, c; Yurkov et al. 2015b; Millanes et al. 2016; Begerow et al. 2018; Haelewaters et al. 2020b; Li et al. 2021).

Species concepts and species recognition

Description and delimitation of dimorphic taxa in Cystobasidiomycetes require detailed observations of macro- and micromorphological structures, including basidiomata, basidia, basidiospores, hyphae, conidia, and haustoria (Oberwinkler 1990; Millanes et al. 2016). Most species have been described based on morphological data; sequence data have been generated only for a few species. Yeast species description and delimitation require culturing of the fungus, description of colony- and cell morphology, physiological characteristics, and molecular phylogenetic analyses (Haelewaters et al. 2020b; Li et al. 2021).

Conclusion and recommendations

Different criteria have been applied for species delimitation in Cystobasidiomycetes: morphology for dimorphic taxa, and culture morphology and physiological characteristics for yeast taxa. Currently, an integrative approach is in use, combining independent evidence from molecular phylogenetic analyses along with the more traditional characters mentioned above. Cystobasidiomycetes comprises both dimorphic species and species only known as asexual yeast stages. Several dimorphic species have been described based on morphological data only, and sequence data are available for few species only. Efforts should be made to isolate dimorphic species in pure culture, to describe the asexual yeast stage, and obtain sequence data of multiple loci.

Species delimitation in Microbotryomycetes

Microbotryomycetes comprises seven orders (Heitmaniales, Heterogastridiales, Kriegeriales, Leucosporidiales, Microbotryales, Rosettozymales, Sporidiobolales), eleven families (Camptobasidiaceae, Chrysozymaceae, Colacogloeaceae, Heitmaniaceae, Heterogastridiaceae, Kriegeriaceae, Leucosporidiaceae, Microbotryaceae, Rosettozymaceae, Sporidiobolaceae, Ustilentylomataceae), 44 genera, and about 300 species (Wang et al. 2015c; Begerow et al. 2018; Denchev et al. 2019, 2020; He et al. 2019; Kemler et al. 2020; Li et al. 2021). It is a diverse class, containing mycoparasites, plant parasites, and saprotrophic yeasts with largely distinct ecological, morphological, and ultrastructural features. Most representatives are dimorphic, although many species are known only from a yeast stage. Only a few taxa are known exclusively as filamentous fungi. The majority of parasitic species alternate between haploid yeasts, which are sometimes called sporidia, and a dikaryotic hyphal stage. The diploid stage is (very) short-lived and generally only observed right before the formation of basidia. In general, parasitism is initiated after somatogamy of two haploid gametes of compatible mating type to form infectious hyphae. The haploid gametes can proliferate as yeasts, and it is assumed that species that exist only as yeasts are derived.

The class Microbotryomycetes was erected to accommodate a heterogenous group of organisms and is only phylogenetically well supported (Bauer et al. 2006). No synapomorphic morphological character has been found. Morphologically, basidiomata vary from stilboid and pycnoid forms, and the class includes parasitic fungi that do not form their own basidiomata but rather grow in or between tissues of their host species. Plant-parasitic species

in Microbotryales produce macroscopic sori in species-specific tissues of their host plants (Kemler et al. 2020). Basidia are generally transversely septate, producing ballistosporic basidiospores. Some species produce conspicuous conidiophores and conidia (e.g., in *Colacogloea* and *Krieglsteinera*). Some taxa have unique structures, such as the conspicuous multirooted basidiophores in *Krieglsteinera lasiosphaeriae*, or large, tetrahedral basidiospores in *Heterogastridium pycnoideum*.

At the ultrastructural level, various yeasts and mycoparasites are characterized by the presence of colacosomes, also referred to as lenticular bodies (Bauer and Oberwinkler 1991a). Colacosomes of Microbotryomycetes seem to have a different ontogeny and content than those of Cryptomycocolacomycetes (Bauer et al. 2004; Oberwinkler et al. 2017). The diversity of colacosome-forming Microbotryomycetes is large, comprising asexual yeasts (e.g., *Sporobolomyces johnsonii*), filamentous fungi (e.g., *Heterogastridium pycnoideum*), and dimorphic fungi (e.g., *Colacogloea effusa*). The two major ecological strategies in the class are myco- and phytoparasitism, of which mycoparasitism is phylogenetically more widespread and likely represents the ancestral ecological strategy of the class. Thus far, it remains difficult to infer ecological functions of asexual yeast species.

Mating initiation in plant parasites is controlled by a pheromone–pheromone–receptor system with two mating types (MAT A1 and MAT A2). Although not experimentally shown, genome analyses indicate that subsequently homeodomain transcription factors mediate a successful dikaryotization (Branco et al. 2018). After successful mating, infectious hyphae are produced in the plant parasitic species that infect their host via an appressorium through the epidermis (Schäfer et al. 2010). Although many population studies support clearly separated species, hybrids between closely related species are observed in nature (Petit et al. 2017). Hybrids can also be producted in culture under laboratory conditions, but their infection rate is apparently markedly reduced (Büker et al. 2020).

Species concepts and species recognition

New species within the class Microbotryomycetes are mainly described based on molecular phylogenetic data. In the case of parasitic species, host information is also often used as a separate lineage of evidence. Yeast species are often described with additional physiological data in the form of assimilation studies. Species delimitation within the class varies between the three major functional groups:

Yeasts Species delimitation of organisms exclusively known as asexual yeast-forming fungi is mainly based on an integrative approach incorporating physiological characteristics, multilocus phylogenetic inferences, and morphological data (e.g., Wang et al. 2015c; Li et al. 2021). For unambiguous species assignment, ITS and LSU loci remain the most important genetic markers.

Phytoparasites For plant parasitic species, macromorphological traits include sorus location, formation of a columella, and spore mass coloration. Microscopic characteristics include teliospore size, teliospore ornamentation, and formation of disjunctors between teliospores. Hyphal growth of plant-parasitic species is intercellular and specific interaction structures are unknown. An important aspect for plant-parasitic species is host data. Host specificity as a characteristic for species delimitation in the Microbotryaceae—especially in the genus *Microbotryum*—has been debated for quite some time. Recent molecular phylogenetic work demonstrates that host specificity is very high. Therefore, most recent species descriptions in the family are not based on the discovery of new material, but on the recognition that most species previously thought to have a broad host spectrum, actually contain many cryptic species. However, there are exceptions: *Microbotryum* anther smuts on Caryophyllaceae hosts (Caryophyllales) have a generally very high host specificity. Yet, just a few *Microbotryum* species parasitize several dozens of *Dianthus* species (Caryophyllales, Caryophyllaceae) (Refrégier et al. 2008; Denchev et al. 2009; Kemler et al. 2013).

Mycoparasites Delimitation of mycoparasitic taxa in this class is mainly based on a morphological species concept, involving detailed observations of micromorphological structures, including the shape and dimensions of basidia, basidiospores, conidiophores, conidia, and hyphal system, as well as the presence or absence of clamps (Hauerslev 1993; Bandoni et al. 2002). Basidiomata of mycoparasites are highly variable, and various species have lost the capability to form their own basidiomata. These species rather grow between the tissues of their host fungus and are referred to as "intrahymenial" Basidiomycota. Information about host species identity has not been used consistently for species delimitation—it remains unclear to what extent mycoparasites of Microbotryomycetes are host specific. Sequence data are available for few species only and consequently have only been used sporadically in species descriptions (e.g., Toome and Aime 2014).

Oberwinkler et al. (1990) proposed the genus *Colacogloea* for *Platygloea peniophorae* based on the detection of colacosomes. Subsequently, various mycoparasites that were found to produce colacosomes were combined or newly described in this genus. However, none of these studies were (originally) supported by sequence data, and decisions were made based on morphological features alone (Kirschner et al. 2000; Bandoni et al. 2002). Recently, several species exclusively known as a yeast stage were assigned to this genus based on molecular phylogenetic reconstructions (Wang et al. 2015c; Li et al. 2021).

Conclusion and recommendations

Currently, different species concepts are being applied in Microbotryomycetes; this generally depends on the functional group that is being studied (integrative species concepts in yeasts and plant parasites vs. a mainly morphological species concept in mycoparasites). Species delimitation in asexual yeasts is based on the integration of molecular sequence data, morphological data, and physiological characteristics, whereas species delimitation of plant parasites involves morphological, ecological, and host information, supported by molecular phylogenetic inferences. Finally, species delimitation of mycoparasites has traditionally been based on (micro-)morphological characters, sometimes combined with host species information. Datasets of morphology, ecology, and sequence data are currently too fragmentary among the major functional groups of Microbotryomycetes, to be able to establish criteria for a class-wide species concept. An integrative approach for species delimitation incorporating genomic data and detailed observations on morphology and ecology is paramount to improve our insights in Microbotryomycetes diversity.

Species delimitation in Pucciniomycetes

Pucciniomycetes is by far the largest class of Pucciniomycotina, containing over 8000 species (Aime et al. 2014). The vast majority of them belong to Pucciniales, the order that exclusively contains the obligate plant-parasitic rust fungi. Species of Pucciniales are most commonly found in their urediniospore stage which re-infects the host during the growth season. Rust fungi usually form yellow, orange, or brown pustules on leaves, stems, and fruits, giving the infected areas rust-like appearance. However, some species can also induce gall formation, deformed plant growth, and even pseudoflowers (Cummins and Hiratsuka 2003). The other members of Pucciniomycetes are morphologically different from rusts, but most of them are parasitic—infecting mosses, scale insects, fungi. Members of Septobasidiales form dense fungal mats on scale insects; Platygloeales form minute fruiting structures on mosses and ferns; and Helicobasidiales form fungal mats on tree roots and they parasitize rust fungi. The monotypic Pachnocybales is the only order that is known to be saprotrophic but further studies are needed to unveil the diversity in this group and better understand their biology (Aime et al. 2014).

While some of the morphological characters (e.g., size and shape of teliospores and spermogonia) are considered useful characteristics for genus- and species-level identification of some rust fungi, other spore stages, or host association, are not always informative. This has led to more than 17,000 species and over 2000 subspecies names in MycoBank (https://www.mycobank.org), many of which are considered taxonomic synonyms. While navigating all these names can be confusing, determining the correct name is crucial in Pucciniomycetes as many rust fungi are economically or ecologically important plant parasites. The use of different names for the same species and unresolved taxonomic treatments may result in delayed decision-making and management, and ultimately in missed opportunity for prompt actions.

Species concepts and species recognition

For the identification of species of Pucciniomycetes, host information is the most important character, followed by teliospore morphology. Spore morphology is the primary character to delimit species of Pucciniomycetes, whereas sorus morphology is used to delimit higher taxa (e.g., Couch 1938; Cummins and Hiratsuka 2003; Aime et al. 2014). However, the application of morphology is challenging as it is mostly based on simple characters that often overlap (Liu et al. 2013; Savchenko et al. 2014a, b; McTaggart et al. 2016; Demers et al. 2017). Also host range alone is insufficient for species delimitation; morphological and molecular phylogenetic evidence have led to expanding the host range of given species (Ebinghaus et al. 2018) but also the opposite—splitting taxa thought to have a broad host range into species parasitizing single hosts (Berndt 2011; McTaggart et al. 2015b). DNA barcoding and phylogenetic methods are very much used in an integrative approach to delimit species nowadays (e.g., Tian et al. 2004; Zhao et al. 2015; Ebinghaus et al. 2018; Léveillé-Bourret et al. 2021). Since it can be challenging to obtain sequence data from old herbarium specimens, epitypification from fresh collections and thorough molecular studies of all materials (especially of the ones with few morphological characters) is essential for accurate species delimitation and recognition in Pucciniomycetes.

Although it has been used for species delimitation of some groups (Weber et al. 2002; Szabo 2006; Chatasiri et al. 2006; Alaei et al. 2009), the ITS region is not an effective barcode for rust fungi; intra-specific and intra-individual variation are observed in a wide range of taxa potentially misleading identification, but it is also difficult to amplify without rust-specific primers and the presence of indels inhibits direct sequencing (McTaggart and Aime 2018). The LSU has been used as an alternative barcode for rust fungi instead, alone or with other markers (e.g., Bennett et al. 2011; McTaggart et al. 2015a; Maier et al. 2016; Ebinghaus et al. 2018). Depending on the genus, different barcodes may provide better species resolution (see discussion in Bubner et al. 2019). McTaggart and Aime (2018) wrote for *Coleosporium* that the ITS2 spacer region may vary where LSU is unable to differentiate among species. The authors proposed the use of the combined ITS2–LSU rDNA region to resolve species complexes and provide species-level identifications for rust fungi. Finally, it may be possible that new barcodes be developed based on the generation of genome scale data (Aime et al. 2018a).

Conclusion and recommendations

Examination of morphological characters is still important in Pucciniomycetes, especially for the rust fungi because the vast majority of rust species have not been sequenced. As a result, the lack of matches in DNA sequence databases does not mean that a given fungus represents an undescribed species, and careful examination of earlier records of rusts from the same host species needs to be performed. For both genus- and species-level delimitation, phylogenetic reconstructions of various loci of ribosomal and mitochondrial DNA are often conducted (e.g., Vialle et al. 2013; McTaggart et al. 2015a; Doungsa-Ard et al. 2018). Thorough molecular revisions are needed at the species level, based on phylogenetic analysis of the ITS2–LSU region (McTaggart and Aime 2018) and in combination with secondary barcodes, as some studies of rust fungi have uncovered a great number of species complexes and cryptic species. For example, analyses of the *Melampsora epitea* complex from northwestern North America determined the existence of 14 different phylogenetic species (also termed "phylotypes") within this single morphospecies (Bennett et al. 2011) and studies within the *Endoraecium digitatum* (Berndt 2011) and *Dasyspora gregaria* (Beenken et al. 2012) species complexes have revealed similar patterns of cryptic speciation. It is recommended to evaluate the suitability of already existing names when describing new species. This is one of the challenges that researchers who work with rust fungi need to face because often the type collections are in poor condition or present only few morphological characters. Moreover, since the DNA extractions from old herbarium specimens of rust fungi have a low success rate, it might be impossible to obtain DNA sequences for certain types.

Species delimitation in Spiculogloeomycetes

Spiculogloeomycetes was established by Wang et al. (2015c) based on a seven-locus phylogenetic reconstruction of Pucciniomycotina. This relatively small class contains intrahymenial dimorphic mycoparasites of the genus *Spiculogloea* and anamorphic yeasts mainly of the *Sporobolomyces subbrunneus* group. The class contains one order (Spiculogloeales), one family (Spiculogloeaceae), three genera (*Meniscomyces*, *Phyllozyma*, and *Spiculogloea*), and at least 15 species (Begerow et al. 2018; He et al. 2019; Li et al. 2021).

Species concepts and species recognition

The genus *Spiculogloea* was described to accommodate *S. occulta*, an intrahymenial parasite of *Hyphoderma argillaceum* (Polyporales, Meruliaceae) from Mallorca (Roberts 1996). This species is characterized by transversally septate basidia covered with small spicules that emerge from small, ornamented probasidia, the presence of conidia, and clamped hyphae. Interaction with the host is made through tremelloid haustoria, which form nanopores at the contact surface. Four more mycoparasitic species have been described within *Spiculogloea* from various host species (Hauerslev 1999; Roberts 1997; Trichiès 2006; Schoutteten et al. 2018). Species of *Spiculogloea* do not produce basidiomata and all have ornamented, transversally septate basidia. Species delimitation is based on shape and dimensions of micromorphological characters—mainly basidia, basidiospores, and conidia. Langer and (1998) reported a yeast stage for *S. occulta*. Sequence data are not available for any of the filamentous species; they are placed tentatively in *Spiculogloea* based on basidium morphology.

Yeast taxa are described and delimitated based on molecular phylogenetic data (mainly based on ITS and LSU sequences) and physiological characteristics. Following this approach, Wang et al. (2015c) recognized five yeast species of the *Sporobolomyces subbrunneus* group as members of the class based on their seven-locus dataset and, consequently, established the genus *Phyllozyma* to accommodate this lineage within Spiculogloeomycetes. Li et al. (2021) described two new yeast species of *Phyllozyma* as well as *Meniscomyces layueensis*, all isolated from phylloplanes collected in China.

Conclusion and recommendations

Since the overlap in available data among dimorphic mycoparasites and anamorphic yeast species in the class is marginal, there is no class-wide consensus with regard to species delimitation. The filamentous mycoparasites are delimited morphologically, based on characteristics of microscopic structures. The description and delimitation of anamorphic yeast species is based on the integration of multiple features—molecular phylogenetic reconstructions, physiological characteristic, and cell- and colony morphology. To bridge the gap between the available data for filamentous vs. yeast taxa in Spiculogloeomycetes, efforts should be made to culture putative new species of dimorphic mycoparasites. The yeast stage can be used for sequencing and should be described following standard procedures (with cell- and colony morphology and physiological characteristics). It is advisable to sequence the seven loci from Wang et al. (2015b, c), because this study presents the best multilocus reference dataset of Spiculogloeomycetes to date.

Species delimitation in Tritirachiomycetes

The genus *Tritirachium* was described by Limber (1940) to accommodate three species, *T. album*, *T. dependens* (type),

and *T. spicatum*. These fungi were at that time classified as Ascomycota in the presently obsolete class Hyphomycetes. Species in the genus are characterized by the presence of long, erect to recumbent, verticillately branched conidiophores with somewhat subulate terminal branches that taper in a distinct zig-zag rachis at which one-celled conidia are formed. *Tritirachium cinnamomeum* was described by van Beyma thoe Kingma (1942), and *T. brumpti* was described based on an isolate from an infected eye of a European girl in Egypt (Langeron 1947). After morphological study, de Hoog (1972) proposed that only two species should be included in the genus, *T. dependens* and *T. oryzae*, under which *T. brumptii* was considered a synonym. Later, he accepted *T. cinnamomeum* and *T. isariae* (de Hoog 1973). Beguin (2010), still only using morphological, physiological, and ecological data, described *T. egenum* to accommodate a biotrophic mycosymbiont growing in close association with *Penicillium rugulosum*. Interestingly, this species could initially not be grown in axenic culture, but using a hot water extract of *Alternaria alternata* allowed growth in vitro.

A major contribution was made by Schell et al. (2011), who generated the first sequence data for *Tritirachium*. Using a dataset of SSU, ITS, LSU, *rpb2*, and *tef1* sequences, the authors discovered that *Tritirachium* did not belong to Ascomycota, but rather to Basidiomycota. Based on the genetic distances observed in the phylogenetic trees, Schell et al. (2011) concluded that the genus should be interpreted to represent class Tritirachiomycetes, order Tritirachiales, family Tritirachimycetaceae. The authors found that the morphological species concept did not accurately circumscribe species boundaries and, hence, they used a phylogenetic species concept recognizing six species: *T. dependens*, *T. oryzae*, *T. roseum*, *T. cinnamomeum*, and two undescribed species that still need to be described. *Tritirachium egenum* was considered a synonym of *T. dependens* (Schell et al. 2011). Beguin et al. (2012) studied sequence divergence of the SSU and found that *T. egenum* is phylogenetically sister to *T. oryzae*, distinct from *T. dependens*. The differences between the results of Schell et al. (2011) and Beguin et al. (2012) are difficult to comprehend and need further investigation. The position of these fungi as a class in Pucciniomycotina was confirmed by Manohar et al. (2014) by multilocus phylogenetic analysis. These authors also described *T. candoliense* isolated from an anoxic zone in the Arabian Sea. Manohar et al. (2014) also compiled the morphological differences among the five accepted species at that time and they could be discriminated. Finally, Bezerra et al. (2020) described *T. batistae* based on ITS, LSU, and *rpb2* sequences. Thus far, most isolates of *Tritirachium* originated from plant materials, but also from clinical and marine habitats, including sponges.

Using SSU sequence data, Beguin et al. (2012) described *Paratritirachium*, a genus with a sister relationship to *Tritirachium*. *Paratritirachium* at that time contained only one species, namely *P. cylindroconium* that previously was classified in *Nodulisporium*, a representative of anamorphic Xylariales (de Hoog 1973). Nguyen et al. (2014) added a second species to the genus, *P. curvibasidium*, for a heat-resistant fungus isolated from flare pit spoils in Canada. This paper describes for the first time a sexual state in Tritirachiomycetes. Basidiomata and clamp connections are absent, but unfused clamp connections occur. Curved basidia originate directly on the hyphae after 1 week of inoculation, and they are pale brown, thick-walled, with oval basidiospores formed on short sterigmata. Hyphae are binuclate and the basidiospores uninucleate (Nguyen et al. 2014).

Species concepts and species recognition

Within Tritirachiomycetes the phylogenetic species concept confirmed previously recognized morphologically recognized species, as well as new species. GCPSR has recently be employed to delimit species. Markers used thus far, both for species delimitation studies and higher taxonomic level relationships, include SSU, ITS, LSU, *rpb2*, and *tef1*.

Conclusion and recommendations

Tritirachiomycetes was only recently recognized as a class in Basidiomycota. The class includes only two genera with eight formally described species. Two undescribed species have been identified in the literature and await formal description. Likely, our knowledge on the biodiversity of the class is limited, given that species have been isolated from many habitats in many regions on the planet. Likely, species of Tritirachiomycetes also occur in indoor environments and may pose a risk for human health. Sampling in extreme, heat, and dry environments is proposed in enriching the diversity within this class.

Subphylum Ustilaginomycotina

Species delimitation in Exobasidiomycetes

The class Exobasidiomycetes comprises about 650 species in 56 genera, 21 families, and nine orders (Ceraceosorales, Doassansiales, Entylomatales, Exobasidiales, Georgefischeriales, Golubeviales, Microstromatales, Robbauerales, Tilletiales) (Wang et al. 2015a; Begerow et al. 2018; Kijpornyongpan et al. 2018; He et al. 2019). Most of the members are known to be plant-parasitic, but some lineages

comprise insect-associated species and species with unclear ecology. The genus *Tilletiopsis* was used to describe the asexual and saprotrophic yeast species isolated mainly from plant surfaces (Begerow et al. 2000). However, the genus *Tilletiopsis* turned out to be polyphyletic and meanwhile several lineages have been described as individual genera (Wang et al. 2015a; He et al. 2019).

Species concepts and species recognition

Genera in Exobasidiomycetes, including *Entyloma*, *Doassansia*, and *Tilletia*, have always been considered typical smut fungi and species delimitation in these genera has followed the same approach as for parasitic genera in Ustilaginomycetes (see below). A morphological species concept combined with an ecological species concept—focusing on host specificity—is prevalent for species delimitation. As morphological traits are often limited, different authors often make their own interpretations and several attempts have been made to lump or split species of *Exobasidium* (e.g., Döring and Blanz 2000; Begerow et al. 2002). In most lineages, however, only very few species are sampled regularly, and trait variation from different collections within the area of distribution has been rarely studied. Therefore, molecular phylogenetic data have become the main source of species recognition nowadays. ITS is used as the barcode marker to distinguish among species (Begerow et al. 2014).

A mating system similar to that of *Ustilago* and related species appears to have emerged in Exobasidiomycetes (details below) and the orthologues of two mating loci could be identified in the various genomes. However, comprehensive analyses of the genomes and mating experiments supporting biological species based on intersterility are still lacking.

Conclusion and recommendations

The monograph of smut fungi by Vanky (2011), including five of nine orders, and the morphological species concept used therein was mostly supported by phylogenetic approaches. Animal-associated asexual species in Exobasidiales could only be included based on molecular data. Lineages like Ceraceosorales, Golubeviales, and Robbauerales are only known with very few asexual species and accepted based on long branches. Thus, delimitation in Exobasidiomycetes is as diverse as the group itself. The extensive use of ITS and LSU—as the most relevant markers—provides a comprehensive dataset. However, some closely related species like the economically important *Tilletia* species on barley, wheat, and rye will need more detailed studies to accurately distinguish among species. In addition, these species groups hint at a much higher diversity than anticipated by phenotypic data alone.

Species delimitation in Malasseziomycetes

The class Malasseziomycetes contains one order (Malasseziales), one family (Malasseziaceae), and one genus, *Malassezia*. This genus was described by Baillon (1889) and initially only two species were recognized, the lipid-dependent *M. furfur* (type) and the lipophilic *M. pachydermatis*. The morphological hallmark of the genus *Malassezia* is the unique unipolar mode of budding in which buds emerge only at one pole of the cell with the new bud cell walls erupting through the original cell wall of the yeast cell, leaving (rather) prominent bud scars. Several buds may be formed at this single bud site, making budding percurrent. As a result, most parental cell-bud combinations have a somewhat flask-shape morphology that can also be easily recognized, also when present in, e.g., skin biopsies. Meanwhile, sympodial budding, but only occurring at one pole of the cells, has been reported, e.g., in *M. sympodialis* (Simmons and Guého 1990). This unique morphological feature makes it rather easy to recognize a yeast cell as belonging to the genus *Malassezia*. As of today, the genus contains 18 species (Wijayawardene et al. 2020).

Malassezia yeasts occur as commensals on human skin; they are causal agents of skin disorders such as pityriasis versicolor, seborrheic dermatitis, atopic dermatitis, folliculitis, and dandruff; and they have been reported to cause sepsis in patients (pre-term babies, immunodeficient adults) who receive parenteral nutrition via a catheter (Boekhout et al. 2010; Gaitanis et al. 2012; Iatta et al. 2018; Theelen et al. 2018; Rhimi et al. 2020). In a 1-year hospital study in Italy the incidence of *Malassezia*-related sepsis was 2.1% among cases of expected candidemia (Iatta et al. 2018). Because of the involvement of several species in various skin disorders (e.g., *M. furfur*, *M. globosa*, *M. sympodialis*, *M. restricta*) and sepsis (*M. furfur*, *M. pachydermatis*, *M. sympodialis*), correct species identification is important. This was emphasized as part of recently published clinical guidelines (Arendrup et al. 2014). We believe that the number of invasive *Malassezia*-related infections is vastly underreported as the special media required for their growth are not used in routine clinical microbiology laboratories (Iatta et al. 2018).

Malassezia globosa and *M. restricta* are widely involved in skin-related disorders at a global scale. As a result, many pathobiological studies focus on these two species (Gaitanis et al. 2012; Grice and Dawson 2017; Theelen et al. 2018). Moreover, their dermatological importance made that the genomes of these two species were the first to be published (Xu et al. 2007), later followed by the genomes of most other species (Wu et al. 2015). Meanwhile, the description of the recently described species *M. verpertilionis* from Myotinae bats in the USA was accompanied with the characterization of its genome sequence (Lorch et al. 2018). *Malassezia* yeasts are also important because they cause skin infections

in other warm-blooded animals, including pets (Table 1). For instance, *M. pachydermatis* is the main causal agent of dermatitis and otitis in dogs and cats (Cafarchia et al. 2005; Sugita et al. 2010; Bond et al. 2020).

Until recently, the taxonomic position of *Malassezia* was not settled, but an affinity with the basidiomycetous yeasts was inferred based on the presence of enteroblatic mode of budding, the presence of urease activity, and a positive Diazoneum Blue B salt reaction (Guého-Kellermann et al. 2010, 2011). Based on the phylogenetic analysis of the LSU alone or in combination with protein-coding genes, it was proposed that the genus belongs to Ustilaginomycotina (Begerow et al. 2000, 2006; Xu et al. 2007), where it was classified within the order Malasseziales in Exobasidiomycetes. An alternative proposal placed it in Ustilaginomycetes (Matheny et al. 2007). Hibbett et al. (2007) treated Malasseziales as Ustilaginomycotina *incertae sedis*.

Wang et al. (2014) expanded the previously used set of loci to better understand the phylogenetic position of the genus within Ustilaginomycotina. To study the taxonomic position of *Malassezia*, they used three datasets: a nuclear rDNA dataset including the complete SSU, ITS, and the LSU D1/D2 domains; a protein-coding dataset including *rpb1*, *rpb2*, and *tef1*; and a combined six-locus dataset. Four monophyletic clades were resolved within Ustilaginomycotina: the two classes Exobasidiomycetes and Ustilaginomycetes, a *Malassezia clade*, and a *Moniliella* clade. Based on their work, Wang et al. (2014) proposed to classify the genus *Malassezia* in its own class Malasseziomycetes in Ustilaginomycotina. Later, based on their seven-locus dataset—also including *cytb*—the distinctness of the *Malassezia* lineage was confirmed among many species of Ustilaginomycotina (Wang et al. 2015a). A genomic-scale analysis with 29 isolates representing 14 species placed Malasseziomycetes basal to Exobasidiomycetes and Ustilaginomycetes, which both are mostly plant-inhabiting lineages (Wu et al. 2015). Kijpornyongpan et al. (2018) were unable to confidently place Malasseziomycetes within the Ustilaginomycotina, a result that was linked to the extreme divergence of this class from other members of the subphylum (animal-associated, small genome sizes).

Unique morphological features support the isolated position of Malasseziomycetes among Ustilaginomycotina. These are the monopolar mode of budding, the thick helicoidal cell walls, and the lipid dependency of most *Malassezia* species (Guého-Kellermann et al. 2010, 2011; Table 1). The affiliation with warm-blooded animals is also unique within the subphylum—and suggests a highly specialized mode of evolution of these yeasts. This may be illustrated by extensive differences in the enzyme profile among the animal- and plant-associated members of Ustilaginomycotina (Xu et al. 2007).

Species concepts and species recognition

For a long time, only two species were recognized (*M. furfur*, *M. pachydermatis*) that could be separated based on the ability, or lack thereof, to grow on regular mycological growth media without the supplementation of lipids. Simmons and Guého (1990) recognized another, lipid-dependent, species, *M. sympodialis*, particularly based on a different mode of budding, namely sympodial rather than strictly percurrent. A major step forward was made when molecular characters became available, especially the LSU, and their use in phylogeny (Guého et al. 1996). In this landmark paper, four new species were introduced: *M. globosa*, *M. obtusa*, *M. restricta*, and *M. slooffiae*. Two of these species—*M. globosa* and *M. restricta*—were found to be the main species involved in many skin disorders that before were thought to be caused by *M. furfur*. The circumscription of these species was also supported following the non-sequence-based identification system as proposed by Guillot et al. (1996), using phenotypic (colony morphology, yeast cell morphology, ultrastructural details of cell walls) and physiological features (presence of catalase activity, growth at 37 °C, and the ability to utilize Tween 20, 40, 60, and 80). Later, 11 other species were recognized mainly based on differences in rDNA sequences resulting in 18 species that are presently recognized (Table 1). This number likely is an underestimation of the true diversity of *Malassezia* species; metabarcoding studies based on ITS sequences have revealed various lineages that could not yet be identified as known species (Amend et al. 2012; Amend 2014).

Phylogenetic studies showed the presence of several clades within the genus. Based on an analysis of the LSU D1/D2 domains, four clusters were observed: (*i*) *M. furfur*, *M. japonica*, *M. obtusa*, *M. yamatoensis*; (*ii*) *M. caprae*, *M. dermatis*, *M. equina*, *M. globosa*, *M. nana*, *M. restricta*, *M. sympodialis*; (*iii*) *M. slooffiae*; and (*iv*) *M. pachydermatis*. Using ITS sequence data, the "*furfur*" and "*globosa*" clades could not be separated (Guého-Kellermann et al. 2010). Analyses of partial sequences of the chitin synthase 2 gene, the LSU D1/D2 domains, and the ITS region were consistent (Cabañes et al. 2005, 2007): the "*sympodialis*" clade with *M. caprae*, *M. equina*, *M. dermatis*, and *M. sympodialis*, with *M. nana* as a basal lineage; the "*furfur*" clade with *M. furfur*, *M. japonica*, and *M. obtusa*; and the "*globosa*" clade with *M. globosa*, *M. pachydermatis, M. restricta, M. slooffiae*, and *M. yamatoensis*. Partial sequences of *rpb1* supported *M. nana* as part of the "*sympodialis*" clade (Cabañes et al. 2007). Although all phylogenetic analyses supported the thus far recognized species, the position of some species, e.g., *M. pachydermatis* and *M. slooffiae*, have remained unclear (Guého-Kellermann et al. 2010).

A phylogenomics approach of 164 Core Eukaryotic Genes (CEGs) resulted in a mostly concordant tree topology

Table 1 Species of *Malassezia* with their hosts and lipid dependency

Malassezia species	Host(s)	Lipid dependency
M. arunalokei	Humans	Lipid dependent
M. brasiliensis	Birds	Lipid dependent
M. caprae	Goats, horses	Lipid dependent
M. cuniculi	Rabbits	Lipid dependent
M. dermatis	Humans	Lipid dependent
M. equina	Cow, horses	Lipid dependent
M. furfur	Birds, camels, cow, dogs, elephants, felids, goats, horses, humans (sepsis), monkeys, pigs, sheep	Lipid dependent
M. globosa	Birds, cow, dogs, felids, horses, humans, sheep	Lipid dependent
M. japonica	Humans	Lipid dependent
M. nana	Cow, dogs, felids, horses	Lipid dependent
M. obtusa	Humans	Lipid dependent
M. pachydermatis	Birds, carnivores, dogs, felids, goats, horses, humans (sepsis), pigs, rhinoceros, sea lions	Lipophilic
M. psittaci	Birds	Lipid dependent
M. restricta	Birds, cow, dogs, felids, horses, humans, sheep	Lipid dependent
M. slooffiae	Birds, goats, horses, humans, pigs, sheep	Lipid dependent
M. sympodialis	Birds, dogs, felids, horses, humans (sepsis), pigs, sheep	Lipid dependent
M. vespertilionis	Bats	Lipid dependent
M. yamatoensis	Humans	Lipid dependent

compared with the LSU D1/D2 tree (Wu et al. 2015; Theelen et al. 2018). Three main clades were retrieved: (*i*) Clade A with *M. brasiliensis*, *M. furfur*, *M. japonica*, *M. psittaci*, and *M. yamatoensis*; (*ii*) clade B with *M. arunalokei*, *M. globosa*, *M. restricta* (=clade B1 in the LSU D1/D2 tree), *M. caprae*, *M. dermatis*, *M. equina*, *M. nana*, *M. pachydermatis*, and *M. sympodialis* (=clade B2); and (*iii*) clade C with *M. cuniculi* and *M. slooffiae*. Sequences of multiple isolates of *M. furfur*, *M. globosa*, *M. restricta*, and *M. sympodialis* showed that they formed monophyletic lineages as expected, and all four but *M. sympodialis* showed some nucleotide polymorphisms.

Intra-specific sequence variation For a correct interpretation of species boundaries, the extent of genetic diversity within these so-called species must be acknowledged. Sugita et al. (2010) compared the amount of divergence in the LSU D1/D2 domains and the ITS1 and ITS2 spacer regions for 13 *Malassezia* species. For all species, sequence similarity of the LSU D1/D2 ranged between 99% and 100%. The similarity of ITS1 and ITS2 sequences was again 99–100% for eight species, but 73–95% (ITS1) and 91–100% (ITS2) for five species (*M. furfur*, *M. globosa*, *M. nana*, *M. pachydermatis*, *M. restricta*). These results indicate that there may be more undescribed species "hidden" within these taxa. Note that for most species with high similarity values, only a few isolates were available. The only exception in this study was *M. sympodialis* that seems to be a well-circumscribed species with limited sequence variation (100% similarity in sequences of LSU D1/D2, ITS1, ITS2).

Extensive genotypic variation was observed in species that are clinically important and, as a result, extensively sampled, e.g., *M. furfur*, *M. globosa*, *M. pachydermatis*, and *M. restricta*, further indicating that these species might represent species complexes, rather than distinct species, but this needs further investigation. Sequence analysis of the intergenic spacer region IGS1 of *M. globosa* showed the presence of 4–8 main clusters, depending on the study, that correlated at least in part with the disease status of the humans from which the isolates were obtained (Sugita et al. 2003, 2010). Single-strand conformational polymorphism analysis of the ITS1 spacer region resulted in five groups of *M. globosa* isolates from pityriasis versicolor patients (Gaitanis et al. 2006).

Intra-species variation for *M. furfur* has been observed for various properties at both the phenotypic and molecular phylogenetic levels. Boekhout and Bosboom (1994) observed four different karyotypes with variation in size and number of chromosomes. Whereas most strains had seven chromosomal bands, strains belonging to karyotype 2 exhibited ten chromosomal bands. The first study that applied AFLP for typing of *Malassezia* species, identified five *M. furfur* subgroups and linked karyotype 2 to a specific AFLP-subcluster. Though the sampling size was rather small, for the first time it was hypothesized that a specific genotype preferentially may invade the body, linking intra-species variation to clinical relevance (Theelen et al. 2001). Another study revealed eight distinct

subgroups in *M. furfur* that to some extent correlated with clinical and geographic origin (Gupta et al. 2004). Gaitanis et al. (2009) found a correlation between PCR fingerprint clustering and the host's geographic origin and underlaying skin condition. A study mainly focusing on *M. furfur* from domestic and zoo animals, observed phenotypic variation as well as multiple sequence-based genotypes for ITS, LSU, and *btub* (Puig et al. 2018). Presence of hybrid genotypes in *M. furfur* was first observed by Theelen et al. (2004), based on AFLP banding-patterns. In a subsequent comparative genomics study, a hybridization event was also suggested based on genome size and double copy number for most genes for some strains of *M. furfur*, which corresponds with karyotype 2 having additional chromosomal bands (Boekhout and Bosboom 1994; Wu et al. 2015). Recently, hybridization events have been widely linked to the rise of new pathogens, as well as to increased intra-specific variation.

Conclusion and recommendations

In Malasseziomycetes, species are delimited based on sequence divergence of the LSU D1/D2 domains, the ITS1 and ITS2 spacers, *rpb1*, *rpb2*, chitin synthase 2, and *btub*, usually in combination with phenotypic differences in cellular morphology, colony morphology, and growth profiles using an array of Tweens. Ecology (host specificity) is an important adjunct to recognize species. Practical species recognition is possible using MALDI-TOF mass spectrometry. Although a sexual stage has not yet been found, genome comparisons revealed a likely functional mating system, which needs to be tested under appropriate experimental conditions. Hybrids occur next to genetically pure species. Several of the currently known taxa probably represent species complexes—e.g., *M. furfur*, *M. globosa*, *M. pachydermatis*, and *M. restricta*. In the future, extensive genome comparisons are needed to better understand the taxonomic structure of these complexes.

In our experience, most *Malassezia* isolates can be identified using sequences of the LSU D1/D2 domains only. However, because several closely related species (e.g., *M. caprae*, *M. dermatis*, *M. equina*, *M. sympodialis*) show highly similar LSU D1/D2 sequences, we recommend to also use ITS sequences for accurate identification. Attempts to use phenotypic methods to identify unknown *Malassezia* isolates are cumbersome and prone to inaccuracies. For instance, Gupta et al. (2004) reported an error rate of 13.8%. Recently, however, MALDI-TOF mass spectrometry has been found to be a useful instrument for the identification of unknown isolates (Kolecka et al. 2014; Denis et al. 2016; Honnavar et al. 2018); to achieve good results, current species libraries have to be made, both with reference isolates and—given the extent of genetic diversity seen in most species—also with locally obtained isolates.

Species delimitation in Moniliellomycetes

Moniliellomycetes contains one order (Moniliellales), one family (Moniliellaceae), and one genus (*Moniliella*) with 17 described species. The genus *Moniliella* was described to accommodate two species of black yeasts, *M. acetoabutens* (type) and *M. tomentosa* (Stolk and Dakin 1966). These species were recognized based on morphological differences, such as presence or absence of chlamydospores and size of arthroconidia. In 1979, a series of articles were published on *Moniliella* and the putative allied genera *Hyalodendron* (nowadays in Tremellomycetes, Trichonosporales) and *Trichosporonoides* (currently synonymized with *Moniliella*), based on morphology, growth profiles, cell wall carbohydrate composition, and production of volatiles (de Hoog 1979; de Hoog and Roeijmans 1979; Martinéz 1979; Martinéz and de Hoog 1979; Martinéz et al. 1979; Weijman 1979). Species of *Hyalodendron* possess xylose in their cell walls, whereas those of *Moniliella* and *Trichosporonoides* lack this compound, and have glucose, galactose, and (low) mannose, but with erythritol and unidentified polyols. *Moniliella* species are capable of fermentation, which is a very uncommon feature among Basidiomycota (de Hoog et al. 2011). de Hoog and Guého (1984) revealed that several species of *Moniliella* differed widely in the percentage of GC content with values ranging from 45.8% to 62.5%. *Trichosporonoides* was synonymized under *Monilliella* by LSU D1/D2 sequence analysis (Rosa et al. 2009), confirming previous suggestions based on morphology (Boekhout 1998; de Hoog and Smith, 1998a, b).

Different species have been recovered from different substrates, including tobacco, juices, syrups, fats, oils, and acids. Some species have also been found from flowers (Thanh et al. 2013; Thanh and Hien 2019). Often the substrates have low water activity and some of the species are known to be xerophilic (e.g., Hocking and Pitt 1981). Some species are involved in industrial alcohol processing (Burschäpers et al. 2002; Kobayashi et al. 2015), whereas others are of medical and veterinary importance (McKenzie et al. 1984; Pawar et al. 2002). Under culture conditions, *Moniliella* species grow in yeast-like, pseudohyphal, or hyphal form, with hyphae forming arthro- and blastoconidia (de Hoog et al. 2011). The placement of the genus within Basidiomycota remained unclear for a long time, mainly due to conflicts among various phenotypic features. The systematic position of the genus *Moniliella* remained unclear until a few years ago, as they share a similar cell-wall composition with other members of Ustilaginomycotina, but several species develop a dolipore that is more similar to septal pores of Agaricomycotina than those

of Ustilaginomycotina (Haskins 1975; Weijman 1979). Only the application of molecular phylogenetic methods resolved the position of this clade—as its own class within subphylum Ustilaginomycotina (Wang et al. 2014).

Species concepts and species recognition

Phylogenetic analysis of Moniliellomycetes is based on multiple DNA markers, mainly the rDNA loci (SSU, ITS, LSU) and protein-coding genes *cytB*, *rpb1*, *rpb2*, and *tef1* (Thanh et al. 2012, 2013, 2018; Wang et al. 2014, 2015a; Thanh and Hien 2019). Species are mainly delimited by the LSU D1/D2 domains and ITS, as well as methylation-specific PCR fingerprinting profiles. In addition, physiological characteristics are used for species delimitation.

Conclusion and recommendations

Moniliella species share several morphological and physiological traits, which justifies their treatment in one genus. Genetically, the genus is very heterogeneous with large genetic differences among individual species; further studies might result in systematic revisions at higher taxonomic levels (e.g., Thanh et al. 2018). In Moniliellomycetes, species are delimited based on a combination of sequence analysis of the rDNA, mainly the LSU D1/D2 domains and the ITS1 and ITS2 spacers, and phenotypic differences in cellular morphology, colony morphology, physiological growth profiles using an array of carbon and nitrogen sources, and fermentation of sugars. A sexual stage is still unknown, and, hence, the biological species concept has not been used. However, genome comparisons will likely uncover the mating locus structure and provide strategies to investigate sexual reproduction. Also, it can be expected that comparative genomics will improve the understanding of species boundaries in these black yeasts.

Species delimitation in Ustilaginomycetes

Ustilaginomycetes is the largest class within Ustilaginomycotina and contains mostly dimorphic plant parasites (Begerow et al. 2014). Most taxa occur on monocotyledonous plant orders, but Ustilaginomycetes also have a diverse range of dicotyledonous hosts. Some taxa are only known as yeasts. The class comprises four orders (Uleiellales, Urocystidales, Ustilaginales, Violaceomycetales), 17 families, 70 genera, and around 1200 species (Wang et al. 2015a; Begerow et al. 2018; He et al. 2019). Ustilaginomycetes is a well-supported monophyletic group. Generic definitions were traditionally based on morphological traits and host plant identity. Since the advent of molecular methods, generic boundaries are mostly defined using DNA markers, thereby leading to the realization that previously pure yeast taxa could be incorporated into a systematic framework of Ustilaginomycetes. Molecular studies additionally often hint at morphological traits that are synapomorphic for a given monophyletic group (e.g., McTaggart et al. 2016). Due to the large diversity and the scarcity of specimens in most taxa the internal systematics of the Ustilaginomycetes is still not fully resolved, but species in genera are well defined.

Species concepts and species recognition

The vast majority of species in this class are well delimited by morphological, ecological (host plant), and molecular characteristics. Macroscopic traits include general sorus texture and sorus location. Microscopic characteristics are spore size and color, spore ornamentation, and sometimes germination. Ultrastructural features such as septal pore structure or interaction zones are important for the distinction of larger groups (Bauer et al. 1997) but play no role in species delimitation. For molecular-based species delimitation, mainly rDNA loci (ITS, LSU) are used, increasingly combined with additional markers encoding proteins (e.g., *tef1*, GADPH, *atp2*, *btub*). However, data for protein-coding genes is still scarce for most taxa. For species recognition, host identity is still the most important factor and because host specificity of these fungi is assumed to be very high, species descriptions without molecular data are still frequent. Often molecular phylogenetic work subsequently confirms these taxa as individual species.

As in all plant–parasitic Ustilaginomycota, mating is a prerequisite for infection as the infection process is controlled by mating-specific transcription factors. Di- and tetrapolar mating systems are known and, interestingly, mainy species seem to have a three-allelic mating system (Bakkeren et al. 2008; Kellner et al. 2011). With respect to the biological species concept, mating experiments between different species have been conducted. Whereas some species hybridize and even produce spore characteristics following mendelian genetics, most species seem to be not compatible in terms of successful mating (Kniep 1922; Kellner et al. 2011).

Species concepts in Ustilaginomycetes are challenged by the inclusion of haploid yeasts strains as revealed by molecular phylogeny, because typical structures of plant parasitism are lacking (Begerow et al. 2000). Mating partners often could not be identified and it is assumed that these strains represent plant-parasitic species in the haploid phase. Therefore, a phylogenetic species concept as described above is used whenever possible.

Conclusion and recommendations

Molecular studies demonstrate a high host specificity in most Ustilaginomycetes species and this has resulted in splitting species complexes into separate taxa (e.g., Kruse et al. 2018). Ustilaginomycetes provides an excellent example of a successful integrated taxonomy approach for species delimitation—based on morphology, physiology, ecology,

and phylogeny. The diverse nature of dimorphic species can only be dealt with using all available data in each case.

Overall conclusion and future perspectives

As shown in the taxonomic sections above, every single property used to delimit species has its strengths and shortcomings. Given this, the best practice is to delimitate species and publish new taxa based on as many independent lines of evidence as available, that is, by applying a so-called integrative (or polyphasic) taxonomic approach. This is coherent with a unified species concept, also termed the "General Lineage Concept of species" (de Queiroz 2007), in which species are treated as segments of separately evolving metapopulation lineages, which can be delimited by using former species concept criteria as independent lines of evidence (e.g., GCPSR, ecological differentiation, morphological diagnostics, geographic range, etc.).

An emerging theme among fungal taxonomists is the increasing use of DNA sequences in supporting the taxonomic uniqueness of individual taxa (Seifert and Rossman 2010). Phylogenetic analyses based on DNA sequences of a single locus to multiple loci have revolutionized the study of fungal taxonomy and provided strong support for establishing new taxa at different taxonomic levels (Yang 2013). This approach has led to the identification of a large number of new and cryptic species within previously recognized species (O'Donnell et al. 2004; Chen et al. 2011; Short et al. 2013; Hagen et al. 2015; Doungsa-Ard et al. 2018). However, there is no standard as to which loci should be analyzed, how much sequence divergence is needed, and what statistical node support is required to call different strains as belonging to different species (Xu 2020). In the recent review by Matute and Sepúlveda (2019), the mean number of unlinked loci to delimit species was 4 (ranging among studies from 1 locus to 15 unlinked loci). Often, the convenience and operability of DNA markers and the traditions of the specialist taxonomists working on the specific group of fungi play a large role in determining how species are delimited for most fungal groups (Xu 2020).

As sequencing costs are decreasing, whole-genome scale data has begun to be used for phylogenetic analysis of fungi (Hettiarachchige et al. 2015; Dentinger et al. 2016; Leavitt et al. 2016; Sepúlveda et al. 2017; Libkind et al. 2020). Genomic data may be more objective in overcoming most of the shortcomings of traditional single locus or multilocus-based studies. Matute and Sepúlveda (2019) proposed four criteria to identify species boundaries using genome scale data in fungi: (i) mostly reciprocal monophyly, (ii) high concordance among genomic partitions, (iii) lower interspecies differentiation than intraspecific differentiation, and (iv) low shared polymorphism. For genome-based species delimitation to work accurately, a dedicated repository with functions for annotation and comparative searches should be available and filtering and curation protocols should be established to prevent the propagation of misinformation on fungal genomes in the literature (Xu 2020). In addition, whole-genome sequences should be generated for representative specimens of previously described species and the type material of newly introduced species, ultimately leading to a robust dataset of whole-genome sequences for all described fungal species. Whole-genome scale data provide more information at the population level (Liti et al. 2010), but how to use these data to improve species delimitation is still a problem with regard to the analytical methods (Philippe et al. 2011; Choi and Kim 2017). Additional analytical challenges involve adjusting for horizontal gene transfer, gene duplications, and population-level processes to determine the true species phylogeny (James et al. 2020).

As a final note, species are the cornerstone of taxonomy. While there are a number of requirements set out by the *International Code of Nomenclature for algae, fungi, and plants* (Turland et al. 2018) to be followed for a name to be validly published, no official rules exist for species descriptions. Nevertheless, mycologists should document newly introduced species following "community standards" to facilitate their identification for other researchers (Yurkov et al. 2021). In moving forward to describe the fungal diversity present on the planet, mycologists are encouraged to adhere to the following best-practice recommendations:

(i) Multiple collections that preferably represent different geographic localities or substrates, whenever available. Description of (pseudo)cryptic species based on a single collection is generally discouraged.
(ii) Multiple lines of evidence for accurate species delimitation (unified species concept). It is often the case that molecular phylogenetic data alone provide insufficient information to describe new species, as do morphological characteristics on their own.
(iii) DNA barcode sequences deposited in a public repository (e.g., NCBI GenBank). It is also recommended to deposit aligned sequence datasets used to support new species delineations.
(iv) Compliance with local and international regulations to collect, export, and deposit specimens.

For details on any one of these general recommendations, please see the recently published papers by the *International Commission on the Taxonomy of Fungi* (ICTF) on how to identify fungi (Lücking et al. 2020) and how to describe new fungal species (Aime et al. 2021).

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