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Species diversity of Basidiomycota

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Abstract

Fungi are eukaryotes that play essential roles in ecosystems. Among fungi, Basidiomycota is one of the major phyla with more than 40,000 described species. We review species diversity of Basidiomycota from five groups with different lifestyles or habitats: saprobic in grass/forest litter, wood-decaying, yeast-like, ectomycorrhizal, and plant parasitic. Case studies of *Agaricus*, *Cantharellus*, *Ganoderma*, *Gyroporus*, *Russula*, *Tricholoma*, and groups of lichenicolous yeast-like fungi, rust fungi, and smut fungi are used to determine trends in discovery of biodiversity. In each case study, the number of new species published during 2009–2020 is analysed to determine the rate of discovery. Publication rates differ between taxa and reflect different states of progress for species discovery in different genera. The results showed that lichenicolous yeast-like taxa had the highest publication rate for new species in the past two decades, and it is likely this trend will continue in the next decade. The species discovery rate of plant parasitic basidiomycetes was low in the past ten years, and remained constant in the past 50 years. We also found that the establishment of comprehensive and robust taxonomic systems based on a joint global initiative by mycologists could promote and standardize the recognition of taxa. We estimated that more than 54,000 species of Basidiomycota will be discovered by 2030, and estimate a total of 1.4–4.2 million species of Basidiomycota globally. These numbers illustrate a huge gap between the described and yet unknown diversity in Basidiomycota.

Keywords Biodiversity · Fungi · Species number · Taxonomy

Introduction

The number of species are there on Earth was listed in the top 125 scientific questions in 2005 that remains unanswered (Kennedy and Norman 2005; <https://www.sciencemag.org/collections/125-questions-exploration-and-discovery>; Hyde et al. 2020a, b). Fungi constitute a diverse kingdom of eukaryotes, estimated to represent 2.2 million species or possibly up to 13.2 million species (Hawksworth and Lücking 2017; Willis 2018; Wu et al. 2019; Antonelli et al. 2020). Fungi are essential in ecosystems as they decompose and recycle nutrients by breaking down complex organic compounds to simple molecules. Some are symbiotic with plants or with algae forming lichens, and some are parasites of plants, animals or other organisms.

Basidiomycota R.T. Moore 1980 is a lineage of Fungi (Zhao et al. 2017a; Tedersoo et al. 2018). There are clades in Basidiomycota supported by modern systematic studies that correspond to the four subphyla viz. Agaricomycotina Doweld 2001, Pucciniomycotina R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. 2006, Ustilaginomycotina Doweld 2001 and Wallemiomycotina Doweld 2014 (Zhao et al. 2017a; Tedersoo et al. 2018; He et al. 2019; Wijayawardene et al. 2020). These lineages comprise most well-known phenotypic groups which are the mushrooms and puffballs in Agaricomycotina, the rust fungi in Pucciniomycotina, and the smut fungi in Ustilaginomycotina. The phylum Basidiomycota also includes a broad range of dimorphic fungi, which switch between a yeast phase and a filamentous phase, along their life-cycle (Boekhout et al. 2021).

Molecular phylogenetic approaches have revolutionised fungal taxonomy of Basidiomycota in the last decades (Lücking et al. 2021). These advances have greatly enhanced our knowledge of species diversity in Basidiomycota. Based on evidence from molecular data,

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numerous new taxa have been discovered in the past ten years. Besides new taxon discovery, many species identified only by morphology in the past have been reclassified as novel taxa in the molecular era. Some examples from China are (i) the cultivated medicinal mushroom “Linzhi”, first identified as the European species *Ganoderma lucidum* (Patouillard 1907), which is now recognized as *G. lingzhi* (Cao et al. 2012); (ii) the enoki mushroom, formerly the European species *Flammulina velutipes*, presently *F. filiformis* (Wang et al. 2018); and (iii) the black fungus, formerly *Auricularia auricula-judae*, presently *A. heimuer* (Wu et al. 2014).

Molecular analyses aid in discovery of morphologically indistinguishable cryptic species in basidiomycetes, including species of *Tricholoma* (Carriconde et al. 2008; Jargeat et al. 2010; Heilmann-Clausen et al. 2017; Yang et al. 2017), polypores (Carlsen et al. 2011; Korhonen et al. 2018; Peintner et al. 2019), boletes (Sato et al. 2007), and yeasts (Boekhout et al. 2021). The number of fungi might be up to 11-fold greater than currently known if cryptic speciation is considered (Hawksworth and Rossman 1997; Hawksworth and Lücking 2017).

The number of fungal species has been estimated in different ways (Blackwell 2011; Hawksworth and Lücking 2017). Wu et al. (2019) estimated that there could be 11.7–13.2 million species of fungi worldwide based on environmental DNA sequence data. A plant-to-fungus ratio calculated from known plant and macrofungal associations predicted between 53,000 and 110,000 macrofungal species worldwide (including macrofungi in Ascomycota; Mueller et al. 2007). Aptroot and Luecking (2016) used grid-based approaches to estimate there could be 800 species of Trypetheliaceae (Dothideomycetes: Ascomycota) which is a lichenized group restricted to tropical forest and savannah ecosystems. De Meeus and Renaud (2002) predicted up to 25,000 species of Basidiomycota, but no method was indicated.

Available estimates of extant species in Basidiomycota vary because different criteria have been used. The number of described species is feasible and has already been suggested in several global team works. The number of Basidiomycota was mentioned as 31,515 in Ainsworth & Bisby's Dictionary of the Fungi (Kirk et al. 2008). Ten years later, a detailed systematic study recognized more than 36,000 extant species in Basidiomycota (Begerow et al. 2018). The number increased to 41,270 according to the latest outline of Basidiomycota (He et al. 2019).

In this paper, we give overviews for particular groups of basidiomycetes, focusing on species diversity and the progress in discovering new species during the past two decades. Using these results, we estimate how many species will be described in the next decades. Furthermore, we estimate the species number in Basidiomycota worldwide.

Methods of species number estimation

Families of Basidiomycota were divided into five main groups: grass/forest-litter saprobic, wood-decaying, yeast-like, ectomycorrhizal, and plant parasitic taxa. These groups could account for 88% of the known basidiomycetes (Pöhlme et al. 2020).

Nine case studies were selected to represent basidiomycetes within these five groups.

The new species publication rate was calculated by the formula “ $\alpha = (A/B)/12$ ” where “A” is the new species number published during 2009 to 2020, and “B” is the estimated species number in 2008 (Kirk et al. 2008).

We extrapolated the publication rate from the nine case studies to ecologically similar groups of Basidiomycota based on the current taxonomic system of Basidiomycota at the family rank (He et al. 2019). Assuming the constant publication rate in the next ten years, we estimated the number of species in each family by $N = A \times (1 + \alpha)^y$, where A is the number of recognized species in 2020, y is the number of year and α is the publication rate. The estimated species number of each order is listed in Table 11.

Finally, the described species are estimated by different publication rates of each studied group of Basidiomycota.

Case studies

Grass/forest-litter saprobic basidiomycetes

AGARICUS

Agaricus (Agaricaceae, Agaricales) are saprobic fungi characterized by fruitbodies with an annulate stipe and free lamellae that produce dark brown spore prints. They are solitary or gregarious in various habitats, such as in forests, gardens, on roadsides, pastures, manure heaps, or decaying organic matter from sea level up to the vegetation limit in mountainous areas (Cappelli 1984). *Agaricus* occurred around 66 million years ago (Mya) in the tropics and was dispersed to other areas worldwide (Zhao et al. 2011, 2016a, b; He et al. 2017). The distribution range extends to all continents except Antarctica (Parra 2008; Zhao et al. 2011). Certain species of *Agaricus* are favored by people for their nutritional and medicinal properties, such as *A. bisporus* (J.E. Lange) Imbach, the button mushroom, which is the most cultivated species in the world. Similarly, *A. subrufescens* Peck is famous for its antioxidant activities (Llarena-Hernández et al. 2017). Several other *Agaricus* species are collected as wild edible mushrooms, for example, *A. campestris* L.: Fr., *A. augustus* Fr.

and *A. arvensis* Schaeff (Li et al. 2021). However, species belonging to the *A.* sect. *Xanthodermatei* may cause mild digestive upsets, but without serious risks of fatal consequences (Parra 2008; Boxshall et al. 2021).

Agaricus has a long history of taxonomic research. Numerous monographs have been published from different areas mainly based on morphology, and mostly from temperate areas, such as those from Europe (Möller 1950; Pilát 1951; Konrad and Maublanc 1952; Kühner and Romagnesi 1953; Wasser 1980; Cappelli 1984; Parra 2008); from America (Kerrigan 1986; Singer 1986). The most referred monographs on tropical *Agaricus* are those of Heinemann (Heinemann 1956, 1978, 1980), in which descriptions and classifications of tropical species has been largely based on traditional systematics of temperate species.

Until the year 2000, taxonomic classification did not reflect molecular phylogeny of species, and their evolutionary histories had not been studied (Callac and Chen 2018). In the last decade, due to the development of molecular approaches, knowledge of the diversity of *Agaricus* has improved. The first molecular study by Mitchell and Bresinsky (1999) was soon to be followed by other researchers (Challen et al. 2003; Geml et al. 2004; Kerrigan et al. 2005, 2008). Eight temperate sections have been widely accepted in *A.* subg. *Agaricus*: *Agaricus*, *Arvenses*, *Bivelares*, *Chitonoides*, *Minores*, *Sanguinolenti*, *Spissicaules* and *Xanthodermatei*. The structure of the annulus (superous vs. inferous; simple vs. double or two layered), odour, discoloration of context when cut or rubbed and Schäffer reaction (aniline × nitrogen acid) are the major criteria for infrageneric classification. The first monographs to use molecular data are those of Parra (2013) and Kerrigan (2016), which documented the most comprehensive information of temperate species from Europe and North America.

Generally, *Agaricus* species living in tropical or subtropical areas are much less well-studied than taxa in temperate areas. Heinemann (1978, 1980) proposed *Lanagaricus* Heinem. and *Conioagaricus* Heinem. as two predominantly subtropical and tropical subgenera, which indicated that the diversity of *Agaricus* from the tropics would be different from those of temperate areas. ITS-based phylogenetic studies revealed 11 new phylogenetic clades from tropical areas, with more clades than from temperate areas (Zhao et al. 2011). As a result of phylogenetic studies, *Lanagaricus* became a heterotypic synonym of the subgenus *Pseudochitonia*; sections *Trisulphurati* and *Laeticolores*, which were placed in *A.* subgenus *Lanagaricus* by Heinemann (1956), were placed in the subgenera *Pseudochitonia* and *Minores*, respectively in systematic studies of Zhao et al. (2016a, b) and Chen et al. (2017).

During the last decade, the taxonomy of *Agaricus* has developed due to the application of multigene molecular phylogenies, especially using divergence time estimates as additional criteria, which proved to be a useful method to rank and name monophyletic clades (Zhao et al. 2016a, b). A new classification system for *Agaricus* considering stem age as a criterion for standardizing taxonomic ranks was proposed by Zhao et al. (2016a, b). The new system is composed of 5 subgenera and 20 sections. Using the same criteria, one more subgenus and four sections were described in later phylogenetic studies (Chen et al. 2017; He et al. 2018a; Parra et al. 2018).

Species diversity of *Agaricus*

Asia, especially China and Thailand, is the region from which most new species were described during the last decade. Large parts of the studies stem from international collaborations between European and Asian teams (Callac and Chen 2018). In total, 119 new species were described from Asia, representing 63% of the new species described worldwide (Chen et al. 2012, 2015, 2016, 2017, 2019a; Zhao et al. 2012, 2013; Karunarathna et al. 2014; Li et al. 2014a, 2016; Thongklang et al. 2014, 2016; Ariyawansa et al. 2015; Gui et al. 2015; He and Zhao 2015; Liu et al. 2015a, 2020; Wang et al. 2015b; Dai et al. 2016; Kaur et al. 2016; Zhao et al. 2016a, b; Zhou et al. 2016; He et al. 2017, 2018a,b; Hyde et al. 2017; Zhang et al. 2017; Bashir et al. 2018; Mahdizadeh et al. 2018; Hussain and Sher 2019; Phookamsak et al. 2019; Zheng et al. 2019; Cao et al. 2021). Most of these new species were from tropical or subtropical regions, which is a good indication of the potential high species diversity in other unexplored tropical areas.

Fourty two new species were published from the Americas, which is the region with the most descriptions of new species after Asia. Most contributions were from North America, with a monograph on North American *Agaricus* written by a senior mycologist and expert on *Agaricus* (Kerrigan 2016). Some new taxa were described from the Caribbean and South America (Drewinski et al. 2017; Parra et al. 2018).

Twenty new species were described from Europe (Parra et al. 2011, 2014, 2015; Parra 2013; Mua et al. 2017; Parra and Caballero 2017; Mahdizadeh et al. 2018). The majority (20 species) are from the monograph of Parra (2013).

New species were also published from other areas. Seven and three new species were described from Oceania and Africa, respectively. Two of three species described from Africa are also found in Asia (Zhao et al. 2012; Chen et al. 2017). Interestingly, the seven *Agaricus* species described from Australia were of the sequestrate (secotiid) form with an enclosed hymenium. Their phylogenetic analyses suggested that climatic events in Australia could be correlated

with the evolution of sequestrate forms (Lebel and Syme 2012; Lebel 2013). Ten species that are known species, but as new combinations or new names are not accounted here.

Species, especially from tropical and subtropical regions have been better studied and classified in recent years with a comprehensive taxonomic system (Zhao et al. 2016a, b; Chen et al. 2017; Parra et al. 2018; He et al. 2019). Previous studies were preliminary steps to evaluate the species diversity in these regions. Extensive sampling in under sampled areas is necessary. Today, almost 600 species of *Agaricus* are recognized, and this number will likely increase further, since diversity studies in many regions are undergoing, such as in Brazil, Caribbean regions, China, India, Mexico, and Pakistan. On the other hand, numerous species appeared to be widely distributed in different continents (based on the morphology). However, among the hundreds of tropical collections, none are conspecific with temperate taxa (with the exception of *A. endoxanthus* and *A. subrufescens*) (Thongklang et al. 2014; Chen et al. 2016). That indicates that many new cryptic species may be discovered during such a process.

New species publication rate

According to Bas (1991), the number of extant *Agaricus* species worldwide is close to 400. Zhao et al. (2011) recognized 386 species in the genus, including 183 that were tropical species. With 189 new species described from 2010 to 2020, the number of species recognized today exceeds 500 (Callac and Chen 2018; Chen et al. 2019a, b; Hussain and Sher 2019; Phookamsak et al. 2019; Zheng et al. 2019; Liu et al. 2020; Cao et al. 2021). In fact, among the 189 newly described species, with the exception of *A.*

pachydermus (Lebel and Syme 2012), *A. patialensis* (Kaur et al. 2016) and *A. zelleri* (Kerrigan 2016), ITS sequence data is available for all taxa (Table 1; Fig. 1).

Wood-decaying basidiomycetes

GANODERMA

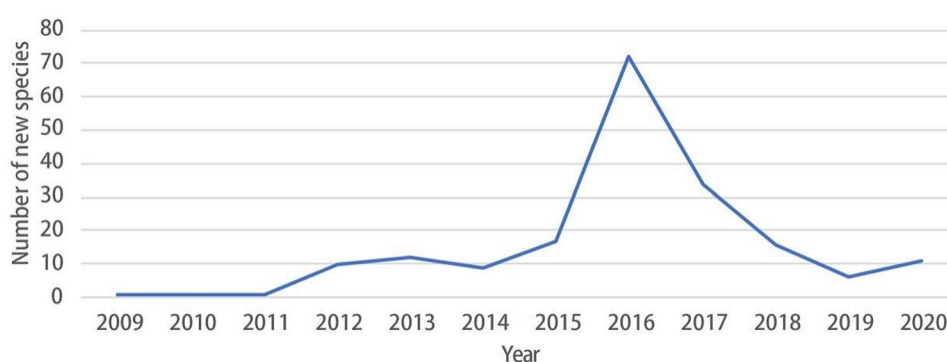
Ganoderma is a large, worldwide distributed polypore genus in the Basidiomycota that includes species causing white rot on various tree species. Recent studies indicated that *Ganoderma* emerged around 60 Mya (Zhu et al. 2015; Tian et al. 2021). The first monograph of ganodermatoid taxa was made by Patouillard (1889), in which he distinguished 29 *Ganoderma* species. A hundred years later, more than two centuries of taxonomic work on this group was summarized by Moncalvo and Ryvarden (1997), with a thorough overview of *Ganoderma* species described before the molecular era. Of the listed 217 *Ganoderma* species (*Ganoderma* and *Elfvingia* were combined) in their study, 148 species were accepted. The majority of these species (ca. 65%) were represented only by one or some few collections restricted to the type locality and adjacent regions (Moncalvo and Ryvarden 1997). This high rate of rare or poorly known species may have been due to the varied morphology of *Ganoderma* fruitbodies, and substandard identification keys based on some arbitrarily chosen morpho-anatomical characteristics used by different mycologists (e.g. Pegler and Young 1973; Steyaert 1980; Moncalvo 2000; Ryvarden 2000; Smith and Sivasithamparam 2003; Torres-Torres and Guzmán-Dávalos 2012).

Table 1 Number of *Agaricus* species published between 2009 and 2020

Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number	1	1	1	10	12	9	17	72	34	16	6	11

New species publication rate 0.0412 (190/384/12)

Fig. 1 Line chart of number of new *Agaricus* species published from 2009 to 2020



Species diversity of *Ganoderma*

Although *Ganoderma* is a well-researched genus, different morphology-based species concepts have resulted in ambiguous species delimitation and identification systems (Moncalvo 2000). Since taxonomists have provided scientific names for more than three hundred *Ganoderma* species described solely on morphology, the re-discovery of already named species is a real problem (Papp 2019). In order to unlock the confused nomenclature and taxonomy in *Ganoderma* and clarify the geographical distribution range of the species, the use of barcoding sequences seems to be necessary. Molecular phylogenetic studies have shown that most of the examined *Ganoderma* species are geographically restricted, in contrast to the earlier theories, which assumed that these species have wide distributions and largely unstructured populations (e.g., Moncalvo and Buchanan 2008; Zhou et al. 2015; Loyd et al. 2018). Phylogenetic studies have also demonstrated that widely used *Ganoderma* names have often been erroneously applied to species described from other biogeographic zones. As an example, Cabarroi-Hernández et al. (2019) found, that *G. weberianum* (Bres. & Henn. ex Sacc.) Steyaert, a species originally described from Samoa (Steyaert 1972) did not occur in the Neotropics, and *G. weberianum* encompassed at least two species, namely *G. mexicanum* Pat. and *G. parvulum* Murrill (Cabarroi-Hernández et al. 2019).

Ganoderma species are important wood-decaying fungi, which grow as facultative parasites of trees, or live as saprobes on dead logs, stumps and roots. The host specificity of *Ganoderma* species is highly variable, but many species show striking host generalism (e.g. *G. adspersum*, *G. applanatum*, *G. curtisii*, *G. philippi*, *G. resinaceum*, *G. zonatum*) (Luangharn et al. 2020). Although numerous *Ganoderma* species have a wide host range, the study of *Ganoderma* species occurring on different trees has recently yielded several new species. As an example, based on a study of *Ganoderma* basidiomes collected on *Jacaranda mimosifolia* in South Africa (Crous et al. 2014; Coetzee et al. 2015), three new *Ganoderma* species were described using nucleotide sequence data. Two new *Ganoderma* species were found by Xing et al. (2018) from the southeast coast of China on living trees of *Casuarina equisetifolia*. *Casuarina* has been reported as a host genus for *Ganoderma casuarinicola* (Xing et al. 2018), but this species was later reported by Luangharn et al. (2019) from Thailand, based on specimens collected on *Pinus kesiya*. A recent study, multilocus phylogeny showed that a bambusicolous species has long been incorrectly identified as *G. neojaponicum* Imazeki in Taiwan, and it is rather a new undescribed species. The new species, *G. bambusicola* is only known from southern Asia and grows on bamboo roots, while morphologically similar *G. neojaponicum* occurs on roots or trunks of conifers in East Asia (Wu et al.

2020). The above examples demonstrate that although most *Ganoderma* species are not host-specific, the host trees and geographical distribution may play an important role in species segregation.

Currently, more than 60,000 tree species are known to science, from which nearly 58% are single country endemics (Beech et al. 2017). Most of these species are known from Australia, Brazil, China, Madagascar, and the largest number of trees is found in the Neotropic biome, followed by the Indo-Malay and the Afrotropic biomes (Beech et al. 2017). Although *Ganoderma* occurs in all forested ecosystems, tropical and sub-tropical regions appear to be the center of its biodiversity. We estimate that nearly 500 species of *Ganoderma* occur globally, of which less than 40% are currently known. Considering this, approximately 300 species await discovery. The vast majority of these will likely be discovered in biodiversity hotspots.

New species publication rate

Different morphology-based species concepts have resulted in ambiguous species delimitation and identification systems in the genus, however, due to the rapid adoption of molecular genetic methods, our understanding of the genetic variability within the genus improved significantly over the last two decades (Papp 2019). Therefore, species boundaries in *Ganoderma* can be re-evaluated based on barcoding sequences, and molecular systematics has been shown to be a valuable tool in current taxonomy (Hapuarachchi et al. 2019). As a result of extensive taxonomic studies on *Ganoderma* mostly performed by phylogenetic methods, 39 new species were revealed in the past 20 years from Africa (Cameroon, Ghana, South Africa), Asia (China, India, Indonesia, Japan, Laos, Thailand), Central America and the Caribbean (Martinique, Mexico) and South America (Colombia, Ecuador, French Guiana, Venezuela) (Hapuarachchi et al. 2018, 2019; Liu et al. 2019; Luangharn et al. 2019; Papp 2019; Tchotet Tchoumi et al. 2019; Ye et al. 2019; Wu et al. 2020; Ryvarden 2020). Currently only 64 *Ganoderma* species are represented by DNA sequence data (Jayawardena et al. 2020). However, based on sequences deposited in GenBank (Sayers et al. 2020) and UNITE (Nilsson et al. 2019), the species number of *Ganoderma* is presumably much higher. Considering the morphology-based observations and the phylogenetic results, He et al. (2019) estimated there are presently 180 extant species in the genus.

Ganoderma has a cosmopolitan distribution, but most of the species are known from tropical and sub-tropical regions. Although, more than 20 *Ganoderma* species have been described from Europe (Moncalvo and Ryvarden 1997), only five well separated clades are confirmed by phylogenetic methods (Beck et al. 2020). Further studies are needed to clarify the species boundaries in the *G. lucidum* complex

(incl. three morphospecies) and the *G. resinaceum* lineage (incl. two genotypes within one morphospecies) (Papp et al. 2017; Náplavová et al. 2020). In order to clarify the laccate *Ganoderma* species present in the United States, more than 500 collections were studied by Loyd et al. (2018), who revealed 12 species using molecular phylogenetic techniques combined with morphological examination. Together with the five additional non-laccate species listed by Zhou et al. (2016), a total of 17 *Ganoderma* species are currently known from the United States. The genus shows a much higher diversity in Asia. As an example, Luangharn et al. (2020) reported 23 *Ganoderma* species only from the Greater Mekong Subregion, out of which three species were new to science. In recent years the genus has been intensively studied in Asia and several new species have been described especially from China (e.g., Cao et al. 2012; Cao and Yuan 2013; Li et al. 2015, 2016; Xing et al. 2018; Hapuarachchi et al. 2018; Liu et al. 2019; Ye et al. 2019). However, the taxonomic position of many previously described species has not yet been settled (e.g., Moncalvo and Ryvarden 1997; Wu and Dai 2005; Papp 2016). However, more species can be expected in the future, especially from the tropical parts of Asia, and many more new species are expected to be found from wooded areas of Africa, Australia, and as well as Central and South America (Table 2; Fig. 2).

Although, no DNA sequence data are available for the majority of currently accepted *Ganoderma* species (He et al. 2019; Jayawardena et al. 2020), several unidentified or mislabelled sequences are deposited at public databases, which represents distinct *Ganoderma* lineages (Papp et al. 2017). In order to estimate the global species richness in *Ganoderma*, an OTU (operational taxonomic unit; Blaxter et al. 2005) abundance dataset was used. ITS sequence data was retrieved from the UNITE database (Nilsson et al. 2019). The dataset contained 2483 ITS sequences representing 160 phylogenetic species (OTUs) at a 98.5% similarity

threshold. The dataset was analyzed based on a Single-Individual-Based rarefaction method in the EstimateS v9 program (Colwell 2013). Based on the result of Chao1 estimator, the estimation number is $(1.9)2.7(4.2)$ times the extant species. This indicate a global estimate for *Ganoderma* of $(342-486(-756))$ species worldwide, 180 of which are currently known. Therefore, the global species richness in *Ganoderma* could be estimated at $2.7 \times 180 \approx 486$ species.

Basidiomycetous yeasts and allied dimorphic taxa in Cystobasidiomycetes, Microbotryomycetes and Tremellomycetes

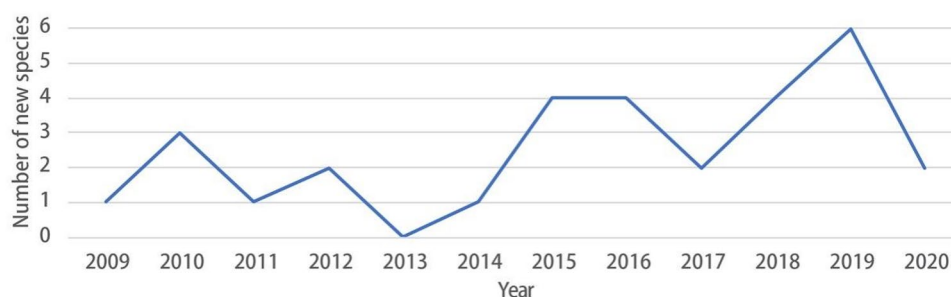
Basidiomycetous yeasts were among the first organisms to be isolated and grown in culture from environmental plants and air samples (e.g., Guillermond 1920; Stark 1921). The ability to grow in a predominantly unicellular form appeared independently in different lineages of Basidiomycota and the ancestor of basidiomycetous yeasts occurred in Cystobasidiomycetes around 330 Mya (Nagy et al. 2014; Zhao et al. 2017a). Identification of these species is based on a few simple morphological characters, such as pigmentation, cell shape and peculiarities of proliferation on artificial media. With the development of microbiological methods, a few important links between yeasts and basidiomycetous taxa were made. The presence of ballistoconidia was observed in the red yeast *Sporobolomyces*. Then, hyphae with clamp connections, and smut-like teliospores were described in the yeast genus *Sporidiobolus* (Nyland 1949). The mating of sexually compatible yeasts and the discovery of mating and a sexual state in *Rhodotorula glutinis* indicated a close relationship between some yeasts and basidiomycetous fungi (Banno 1963, 1967). Other teleomorphic basidiomycetous genera have been described in yeasts, for example *Auricubuller*, *Curvibasidium*, *Cystofilobasidium*, *Leucosporidium*,

Table 2 Number of new *Ganoderma* species published between 2009 and 2020

Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number	1	3	1	2	0	1	4	4	2	4	6	2

New species publication rate 0.0313 (30/80/12)

Fig. 2 Line chart of number of new *Ganoderma* species published from 2009 to 2020



and *Papiliotrema* (reviewed in Kurtzman and Boekhout 2017).

Predominantly unicellular stages, or yeasts, occur in all three sub-phyla of the phylum Basidiomycota: Agaricomycotina, Pucciniomycotina, and Ustilaginomycotina (Hibbett et al. 2007; Boekhout et al. 2011; Kurtzman and Boekhout 2017; Oberwinkler 2017). Many species alternate yeast and hyphal stages throughout their life cycle and were termed as “dimorphic” (Bandoni 1995). The term was introduced by Brefeld in the 1880s to contrast the yeast stage of basidiomycetous fungi having also a dikaryotic hyphal phase from the typical unicellular morphology of sexual ascomycetous yeasts. In dimorphic taxa, the dikaryotic filamentous phase, which forms the basidiomata, is a mycelium that originates from the mating of two compatible strains, and has the potential to form basidia and spores after meiosis. The dikaryotic mycelium grows in nature in association with another fungus (including lichenized fungi) and gain nutrients completely or in parts from the host (Begerow et al. 2017). A teleomorphic state has also been observed in laboratory experiments in several yeast genera, for example *Bulleromyces*, *Curvibasidium*, *Leucosporidium*, and *Papiliotrema* (reviewed in Begerow et al. 2017). Two types of structures responsible for host-parasite interactions were observed in culture, namely, haustoria and colacosomes (reviewed in Begerow et al. 2017). Interestingly, yeasts commonly thought to be saprobes (e.g., *Bullera*, *Cryptococcus*, *Dioszegia*, *Leucosporidium*, *Rhodotorula*, and *Sporobolomyces*) are also known to produce either of these structures. Potential hosts of sexual states of fungi known as basidiomycetous yeasts are often not known, but they can be discovered in the future, as in the case of *Tremella yokohamensis* (Malysheva et al. 2015) and *Phaeotremella foliacea* (Spirin et al. 2018).

Basidiomycetous yeasts are common inhabitants of plant surfaces, aquatic habitats and soils (Peter et al. 2017). The role of saprobic asexual yeast states in successful propagation and vectoring was first recognized in plant parasites. More recently, it has been convincingly demonstrated that asexual species that are closely related to sexual mycoparasites and lichenicolous fungi are widespread in nature (reviewed in Peter et al. 2017; Begerow et al. 2017; Kachalkin et al. 2019). Yeast and filamentous taxa have traditionally been studied by different groups of researchers and therefore the characteristics used have also been completely different: physiology (biochemical characters) in yeasts, and morphology (macro- and micromorphology) in filamentous species (discussed in Begerow et al. 2017; Oberwinkler 2017). Integrated phylogenetic classifications (Liu et al. 2015a, b, c; Wang et al. 2015a) attempted to standardize diagnostic characteristics in both phenotypic groups as much as possible. Even if some groups are currently known to contain only or predominantly yeasts or filamentous stages, a classification based on their life-stage is obviously artificial,

and here we will follow here integrated classifications as far as possible.

The range of fungal hosts for the species with a known filamentous phase in nature is very wide including both basidio- and ascomycetes, but individual Tremellomycetes are usually very host-specific. As examples, *Tremella dactylobasidia* grows associated to the corticioid fungus *Vuileminia macrospora* (Zamora 2009), *Syzygospora lapponica* grows inside the hymenium of *Ascocoryne sarcoides* (Kotiranta and Miettinen 2006), and there are a number of lichenicolous *Tremella* species each growing on a different genus or even species of lichenized ascomycetes (e.g., Millanes et al. 2014a, 2015; Zamora et al. 2016, 2018; Diederich et al. 2018, 2020). Lichenicolous fungi with an assumed dimorphic life-style, can be found among several clades of the Tremellomycetes (Millanes et al. 2011; Liu et al. 2015a, b, c), and the Cystobasidiomycetes, where lichen-inhabiting species are represented only in the genera *Chionosphaera*, *Cyphobasidium* and *Microsporomyces* (Diederich 1996; Millanes et al. 2016a; Černajová and Škaloud 2019; Li et al. 2020a, b). The relatedness between fungi known as yeasts and lichenicolous fungi was demonstrated by Diederich (1996), who was the first to observe and illustrate unicellular budding of spores which is also the first observations of yeast-stages in lichenicolous representatives. Several lichenicolous Tremellomycetes and Cystobasidiomycetes have now been shown to be dimorphic, but the life cycle of lichenicolous taxa is very poorly studied and understood. The spectrum of hosts of lichen-associated taxa is most likely much larger as suggested by recent observations of yeasts not inducing symptoms in their lichen-hosts (Prillinger et al. 1997; Ekman 1999; Lindgren et al. 2015; Spribille et al. 2016; Černajová and Škaloud 2019; Tuovinen et al. 2019, 2021; Mark et al. 2020; Smith et al. 2020). Yeasts detected or isolated from lichens include members of classes Cystobasidiomycetes and Tremellomycetes. Both groups comprise well-studied species of lichenicolous fungi, traditionally considered parasites of lichens (Millanes et al. 2011; Oberwinkler 2017). Lichen-inhabiting yeasts are included in the Cystobasidiales, Erythrobasidiales, and Tremellales. Recently, a potential involvement of yeasts in lichen symbiosis has been suggested as a third partner (Spribille et al. 2016; Tuovinen et al. 2019) and this suggestion is still under debate (Oberwinkler 2017; Begerow et al. 2017; Lendemer et al. 2019; Mark et al. 2020; Hawksworth and Grube 2020; Smith et al. 2020; Tagirzhanova et al. 2021). Although interactions of different nature between lichenized fungi and lichen-inhabiting yeasts are feasible, the specificity of host-parasite associations and dispersal mechanisms of yeast states needs to be clarified to prove the three-party interactions. Consequently, here we use the terms ‘host’, ‘lichenicolous’ and ‘symptom’ without assuming parasitism as the only possible relationship between the partners.

Species diversity of basidiomycetous yeasts and dimorphic taxa in Cystobasidiomycetes, Microbotryomycetes and Tremellomycetes

The number of known basidiomycetous yeasts exceeded 1400 species in 2011 (Kurtzman et al. 2011) and is rapidly growing (Yurkov 2017). The most dynamic taxonomic group is the class Tremellomycetes with 34 new genera, 385 species and 278 taxonomic combinations published in the last 20 years. The majority of these discoveries and changes concern yeast-like taxa and the re-classification of the polyphyletic *Bullera*, *Cryptococcus*, and *Trichosporon* (Liu et al. 2015a, b, c; Li et al. 2020a, b), and the application of the ‘One fungus = One name’ principle to the classification of sexual and asexual states in genera *Bullera*, *Bulleribasidium*, *Cryptococcus*, *Mrakia*, and *Papiliotrema* (Liu et al. 2015a, b, c). A total of 30 new genera, 127 species and 56 combinations in Microbotryomycetes (excluding smuts) were published. As in the previous case, the major changes in that group concern the reclassification of previously polyphyletic genera *Bensingtonia*, *Rhodotorula*, and *Sporobolomyces* (Wang et al. 2015a) and unification of the classification of anamorphic and teleomorphic taxa, e.g., *Leucosporidium*, *Rhodosporidium*, and *Sporidiobolus*.

Taxonomic studies on Cystobasidiomycetes resulted in ten new genera, 43 species and 39 combinations. As in Microbotryomycetes, reclassification of members of genera *Rhodotorula* and *Sporobolomyces* account for the majority of taxonomic novelties (Yurkov et al. 2015a; Wang et al. 2015a). As a result of these recent major reclassification events, several older teleomorphic generic names have been resurrected and/or applied to clades containing also yeast states, e.g. *Carcinomyces*, *Colacogloea*, *Cystobasidium*, *Heterocephalacria*, *Kriegeria*, *Naematelia*, *Phaeotremella*, and *Rhynchogastrea*.

Phylogenetic analyses convincingly demonstrated the polyphyly of a few teleomorphic genera, such as *Cystobasidium* (Millanes et al. 2016a) and *Tremella* (Millanes et al. 2011). *Cystobasidium hypogymniicola* and *C. usneicola* that are distantly related to the type species of the genus *Cystobasidium*, were transferred into a new genus *Cyphobasidium* (Millanes et al. 2016a). Liu et al. (2015a, b, c) suggested to restrict the genus *Tremella* to the clade containing *T. mesenterica* and *T. fuciformis* and reclassified several clades in Tremellomycetes. However, the placement of *Tremella* s. l. clades 1–3 recognised by Millanes et al. (2011) and a few sexual species remained unclear (Liu et al. 2015a, b, c; Kachalkin et al. 2019; Li et al. 2020a, b). Twenty-two *Tremella* species, of which 15 are not related to *Tremella* s. s., have been described between 2015 and 2020. Not only *Cystobasidium* and *Tremella* s. l., but also the genera *Sirobasidium* and *Syzygospora* are highly polyphyletic. *Syzygospora* was previously characterized by holobasidia and

passively released spores. *Syzygospora* s. s. has now been restricted to *S. alba* and *S. pallida* (Filobasidiales, Tremellomycetes), whereas other species have been transferred to the genera *Carcinomyces* (*C. effibulatus*) in Tremellales, *Heterocephalacria* (*H. bachmannii*, *H. physciacearum*, and *H. solida*), and *Piskurozyma* (*P. sorana*) in Filobasidiales (Liu et al. 2015a, b, c). *Sirobasidium* is characterized by basidia arranged in linear chains (de Lagerheim and Paouillard 1892). The phylogenetic position of the type species of *Sirobasidium*, *S. sanguineum*, is unclear because there is no sequence data available for this species, and thus it has not been possible to re-delimit this genus (discussed in Kachalkin et al. 2019).

A review of the geographic patterns of yeasts included examples of organisms with broad and narrow distribution ranges (Yurkov 2017). For instance, a few species of *Vishniacozyma* (e.g., *V. victoriae*, Tremellomycetes) are a good example of ubiquitous plant-related species. The soil yeast *Saitozyma podzolica* (Tremellomycetes) is another example of a widespread species that is linked to a particular type of habitat, moist, acid environments, including acid tropical soils (Yurkov et al. 2012). Species of *Naganishia* can sustain desiccation in deserts and cold environments (Buzzini et al. 2018). Geographic distribution in mild climates in opposite hemispheres and at complementary latitudes was been reported for red-coloured yeasts of *Phaffia* (Yurkov 2017; David-Palma et al. 2020). A similar bipolar distribution showed psychrophilic yeasts in Arctic and Antarctic regions, e.g., members of genera *Glaciozyma* and *Naganishia* (Tremellomycetes). Among yeasts predominantly restricted to a particular type of substrate, *Solicoccozyma* (Tremellomycetes) is a common member of soil communities (Yurkov 2018). Plant surfaces are often inhabited by red-coloured Sporidiobolales (Microbotryomycetes), e.g. *Rhodotorula* and *Sporobolomyces* (Fonseca and Inácio 2006). Despite extensive sampling, a few species have been so far obtained from a single region, being thus good candidates for endemic species. For example, all three species of the genus *Carlosrosaea* (Tremellomycetes) are known from Brazilian bromeliads. *Dimennazyma cistialbidi* (Tremellomycetes) has been isolated only from leaves of a single Mediterranean plant, *Cistus albidus* in Portugal (Inácio et al. 2005). The lichenicolous species are in general widespread and follow the geographical distribution of their lichen hosts. Evidence suggests that speciation in investigated lichenicolous Tremellomycetes and Cystobasidiomycetes is rather driven by host selection rather than by geographical isolation (Werth et al. 2013; Millanes et al. 2014b, 2015, 2016b; Spribille et al. 2016; Diederich et al. 2020).

The number of species in the three classes is rapidly growing, but it is often difficult to directly compare species numbers reported across different studies. Detection, identification, and classification of yeasts have undergone major

changes since the application of gene sequence analyses and genome comparisons (Kurtzman and Boekhout 2017). Phylogenetic analysis is leading to a major revision of yeast systematics and redefinition of nearly all genera (Liu et al. 2015a, b, c; Wang et al. 2015a). In the absence of information on hosts, ultrastructure and life-histories, which are available for teleomorphic taxa, the bulk of solely asexual yeasts has been taxonomically rearranged in phylogenetic hypotheses (Oberwinkler 2017).

Application of ribosomal DNA sequencing for identification of yeasts provided stable characters for recognition of morphologically and physiologically indistinguishable species. As a result of both sampling from the environment and better species discrimination, the numbers of described yeasts doubled in the period from 1998 to 2011 (Lachance 2006). Yeast species cited in earlier works were often identified by different techniques and criteria that may not be as accurate as the current sequence-based approaches. The same constraints, different sampling and isolation protocols, and identification tools, make a direct comparison of regional species richness values and yeast numbers in different substrates impossible. Another difficulty is that many species are documented from only a limited number of strains. Therefore, distribution range and association with a particular substrate, host and vector are not known for many of these fungi.

Recent phylogenetic analyses suggest that many clades in Tremellomycetes, Microbotryomycetes and Cystobasidiomycetes are largely undersampled and represented only by a few species and environmental sequences (e.g., Liu et al. 2015a, b, c; Mašíňová et al. 2017; Kachalkin et al. 2019). Public sequences in GenBank provide good overview of potential new species. Known from very few isolates in culture collections, these yeasts await description, sometimes for decades. A few Tremellomycetes have been isolated in Portugal by Inácio et al. (2002) and re-sampled 20 years later (Kachalkin et al. 2019). The class Microbotryomycetes comprise a number of monotypic genera, which are characterized by a unique characteristic or phylogenetic position, for example *Heterogastridium*, *Kriegeria*, *Libkindia*, *Meredith-blackwellia*, *Pseudoleucosporidium*, *Pycnopulvinus*, *Udeniomyza*, and *Yunzhangia*. The number of species in a few more genera is growing slowly, notably in *Camptobasidium*, *Cryolevonia*, *Hamamotoa*, *Heitmania*, *Yamadamyces*, and *Yurkovia*. Many of these yeasts are slow-growing extremophiles, organisms thriving under conditions that are hard to survive (Buzzini et al. 2018). Consequently, their isolation, cultivation, characterization and preservation are extremely difficult and their diversity is largely underestimated.

Gadanhó et al. (2006) reported members of the tremellomycete genera *Goffeauzyma*, *Naganishia*, *Solicoccozyma*, *Phaeotremella* and the Microbotryomycetes genera *Pseudohyphozyma* and *Rhodotorula* from an acidic pond of the

Iberian Pyrite Belt. The genus *Goffeauzyma* contains a clade of yeasts from extreme acidic environments (Gadanhó and Sampaio 2009; Russo et al. 2010). Only a few fungal species can survive temperatures of 55–60 °C, and none of them are yeasts, which usually grow between 20 and 25 °C (Buzzini et al. 2018). Among a few thermotolerant basidiomycetes, human pathogens of the genus *Cryptococcus* (*C. neoformans* species complex) in Tremellales and Trichosporonales species *Takashimella tepidaria* and *Vanrija thermophila* show a remarkable tolerance to elevated temperatures. Psychrophilic and psychrotolerant species are more common among basidiomycetous yeasts. The tremellomycete genera *Mrakia* (Cystofilobasidiales), *Naganishia* (Filobasidiales), *Gelidatrema* (Tremellales), *Holtermanniella* (Holtermanni-ales) accommodate several prominent cold-adapted yeasts (Buzzini et al. 2018). Members of the genus *Cystobasidium* in Cystobasidiomycetes were also repeatedly isolated from cold habitats. In Microbotryomycetes, several genera are almost exclusively restricted to cold environments. Particularly, the genera *Leucosporidium* (Leucosporidiales), and members of the family Chrysosporiaceae (e.g., *Bannozyma*, *Fellomyces*, *Hamamotoa*) and order Kriegeriales (*Camptobasidium*, *Cryolevonia*, *Glaciozyma*, *Phenoliferia*) show strong affinity to low temperatures. Some of these yeasts can be also isolated from mild climates (e.g., Yurkov et al. 2016, 2020). Nevertheless, many of them remain under-sampled, probably because of the slow growth and complicated culture handling. Extremophile yeasts may, therefore, represent a large proportion of undescribed diversity. Also, knowing physiological preferences of yeast states is important to obtain cultures of lichenicolous fungi and other mycoparasites.

Sexual states of dimorphic basidiomycetes are not always easy to spot in nature. Fruitbodies of witches' butter, *Tremella mesenterica* and a few other jelly fungi are rather large (up to 10–15 cm) and brightly coloured. However, many species of jelly fungi do not have such a remarkable outlook being white, transparent, or dark-coloured, and producing small basidiocarps that are hardly visible when dry (e.g., *Pseudotremella moriformis*, and *Phaeotremella simplex*). Some other tremellalean species are intrahymenial parasites, producing spores within the fruitbodies of their hosts, and are only visible microscopically (e.g. *Tremella giraffa*, *Tremella protoparmaliae*, and *Syzygospora lapponica*).

Ribosomal RNA sequencing helps largely when identifying yeasts and dimorphic taxa. But molecular analyses of mycoparasites and lichenicolous fungi is challenging and may include cloning, design of specific primers and meta-barcoding approaches. Due to the aforementioned constraints, sequences of yeast stages largely outnumber sequences of sexual species, as discussed in Liu et al. (2015a, b, c) and Kachalkin et al. (2019). A combination of two ribosomal DNA-barcodes provides usually reliable

identification results, with the ITS region being, as a rule, more variable than the LSU (Schoch et al. 2012). A few lineages in the Tremellomycetes demonstrated the opposite situation, in spite of the expected greater variability in the ITS region, which is less constrained for mutations (Scorzetti et al. 2002). However, a growing number of available sequences showed that species delimitation with ITS and LSU is sometimes problematic. Studies that utilized multi-locus sequence analyses (MLSA), mating experiments, and genomic analyses revealed cryptic species and species complexes. There are seven closely related species in the pathogenic *Cryptococcus* species complex (Hagen et al. 2015) and three species in the *C. amyloletus* species complex (Passer et al. 2019). The available knowledge suggests that the reliable identification of species in that genus can be achieved by sequencing protein-coding genes (e.g., Passer et al. 2019). An MLS analysis of the *Papiliotrema flavescens* species complex demonstrated a limited utility of ITS and LSU and additionally revealed two novel cryptic species in the complex (Yurkov et al. 2015b). Nucleotide sequences of type strains in *Mrakia*, *Solicoccozyma*, *Saitozyma*, and *Vishniacozyma* allow a formal separation of species in these genera. However, when other publicly available sequences were considered, it was not always possible to set clear borders between closely related species (Scorzetti et al. 2002; Yurkov et al. 2015b, 2020). Specifically, it is unlikely that pairwise comparisons of nucleotide sequences of ITS and LSU will always provide a reliable identification of yeasts comprising the following species complexes, namely *Mrakia gelida* (with *M. frigida* and *M. blollopis*) *Solicoccozyma aerea* (with *S. phenolica* and *S. terrea*), *Saitozyma podzolica*, and *Vishniacozyma victoriae* (with *V. carnescens* and *V. tephrensensis*). There is a good chance that further, and more detailed, studies will reveal cryptic diversity in other clades and genera of Tremellomycetes. In Microbotryomycetes, several species complexes are known, including cold-adapted yeasts in *Leucosporidium scottii* and carotene-producing red yeasts *Rhodotorula glutinis*. Species in the *Rhodotorula glutinis* species complex were delimited using a combination of nucleotide sequences analyses, MSP-PCR fingerprinting, mating assays, and DNA-DNA hybridisation experiments (Gadanhó and Sampaio 2002) and later sequences of pheromone receptor genes (Coelho et al. 2011). Similarly, the psychrotolerant yeasts *Leucosporidium scottii*, *L. creatinivorum*, *L. yakuticum* were demonstrated to comprise a complex of closely related interbreeding species (de García et al. 2015).

A large amount of overlooked diversity is probably also hidden in several species complexes of lichenicolous and mycoparasitic taxa. Millanes et al. (2014b) confirmed that *Biatoropsis usnearum* included several independent lineages some of which were later described as species based on molecular and morphological evidence (Millanes et al.

2016b; Diederich and Ertz 2020), and a few others remain undescribed awaiting for thorough morphological characterization. Other examples of species initially discovered as ‘cryptic’ that have been later characterized and described based on morphological traits include *Tremella cetrariellae* and *Tremella tubulosae* (Millanes et al. 2015; Diederich et al. 2020). Several groups are known to include cryptic diversity, notably *Cyphobasidium* spp. (Cystobasidiomycetes), *Phaeotremella foliacea*, *Tremella macrobasidiata* and *Tremella mayrhoferi* (Tremellomycetes) (Spribille et al. 2016; Zamora et al. 2009, 2016, 2018). Future analyses of host-related, morphological, and molecular data will clarify taxonomic status and diversity of these groups.

New species publication rate

The Dictionary of Fungi (Kirk et al. 2008) listed 14 species in the class Cystobasidiomycetes, 208 species in Microbotryomycetes, and 377 species in Tremellomycetes. Diversity of fungi in Tremellomycetes and Cystobasidiomycetes have substantially increased since then. In a breakdown of diversity of species and genera described during the last ten years, the most species-rich class is Tremellomycetes followed by Microbotryomycetes and Cystobasidiomycetes (Table 3, Fig. 3). The species numbers reflect problems of high-ranking classification in these taxonomic groups. Nearly a half of species described in Microbotryomycetes and Cystobasidiomycetes could not be assigned to any taxonomic order and are presently accommodated in *incertae sedis* genera. In Tremellomycetes, the vast majority of taxonomic novelties were described in the order Tremellales.

Ectomycorrhizal basidiomycetes

GYROPORUS

Gyroporus (Gyroporaceae, Boletales) is a genus of obligately ectomycorrhizal, poroid mushrooms with representatives on every major continent except Antarctica. The genus comprises species with bright yellow spore prints, clamp connections, and the unique condition of having circumferentially (as opposed to longitudinally) arranged stipe hyphae. Members of *Gyroporus* are mycorrhizal with an array of plant species from several plant families including Betulaceae, Fabaceae, Fagaceae, Myrtaceae, Pinaceae and Phyllanthaceae. *Gyroporus* is a boletoid genus in the largely gasteroid Sclerodermatineae (Binder 1999), a sub-order of Boletales notable for exhibiting a diverse array of morphologies and ecologies (Wilson et al. 2011). *Gyroporus* diverged from other lineages in Sclerodermatineae around 61 Mya (Wilson et al. 2012). The iconic European taxa *Gyroporus castaneus* and *Gyroporus cyanescens* have been documented since the eighteenth century, classified

Table 3 New yeast species of Tremellomycetes, Microbotryomycetes and Cystobasidiomycetes published between 2009 and 2020

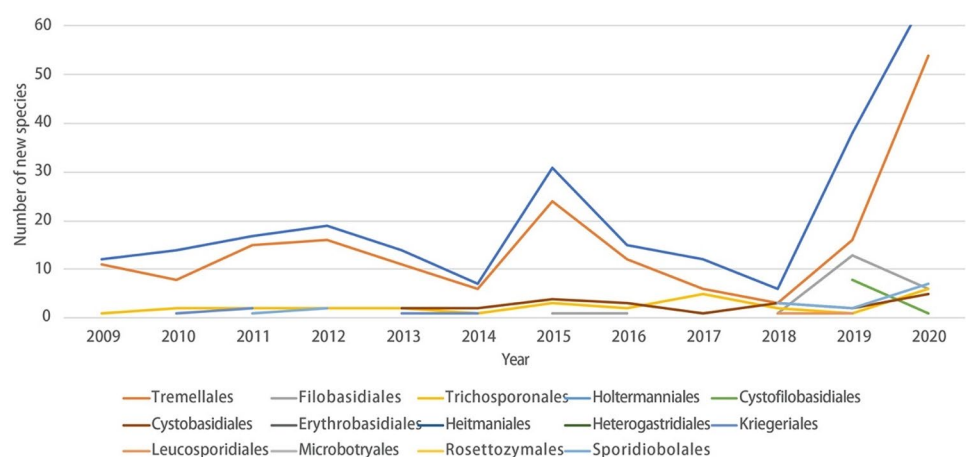
Taxon	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	New species publication rate
Tremellomycetes	12	14	17	19	14	7	31	15	12	6	38	67	0.0557 (252/377/12)
Tremellales	11	8	15	16	11	6	24	12	6	3	16	54	
Filobasidiales					1		1	1		1	13	6	
Trichosporonales	1	2	2	2	2	1	3	2	5	2	1	6	
Holtermanniales		1											
Cystofilobasidiales		3		1			3		1		8	1	
Cystobasidiomycetes	3	1	4		2	2	4	4	1	4	9	11	0.2679 (45/14/12)
Cystobasidiales	2				2	2	4	3	1	3	2	5	
Erythrobasidiales	1										3		
Microbotryomycetes	6	6	5	4	1	3		7	3	5	4	32	0.0304 (76/208/12)
Heitmaniales									3			2	
Heterogastridiales						1							
Kriegeriales		1	2		1	1						2	
Leucosporidiales			1			1		1		1	1		
Microbotryales	6			1								1	
Rosettozymales												3	
Sporidiobolales			1	2						3	2	7	

at that time in *Boletus* (Bulliard 1787, 1788). Despite this long history of formal documentation, many *Gyroporus* species remain to be discovered and described. There are about 35 recognized species (this includes some described varieties not yet formally elevated to species status), which historically have been mostly described from Eurasia, Africa, and North America. The existence of globally distributed semi-cryptic species complexes has hindered progress on properly diagnosing and describing new species. This is especially true for numerous nondescripts,

brown-colored species that are often mistakenly identified as *Gyroporus castaneus*.

Species diversity of *Gyroporus*

Since *Gyroporus* species are described from fruitbodies, the eventual description of all extant species via existing herbarium specimens and further fieldwork is a tractable effort. Also, metagenomic approaches may be a route to estimate and corroborate species diversity. For example, in a study of fungal internal transcribed spacer (ITS) sequences from soil

Fig. 3 Line chart of new yeast species of each order in Tremellomycetes, Microbotryomycetes and Cystobasidiomycetes published between 2009 and 2020

across Australia (Davoodian et al. 2020b), 19 species (operational taxonomic units based on ITS) of *Gyroporus* were inferred from across the continent. Based on Davoodian et al. (2018, 2019, 2020a), ten species of *Gyroporus* are documented from Australia based on phylogenetic analysis of *atp6* and *rpb2* DNA sequences and morphology (including three species yet to be formally described). Considering that ITS sequences can overestimate species diversity given intragenomic variation among copies within some lineages (e.g., Vydryakova et al. 2012; Lindner et al. 2013), it is possible that all species of *Gyroporus* from Australia are known and the task of describing all species is easily achievable. If not, it is possible that further collections are required from areas where fieldwork has been infrequently conducted, such as the Kimberly of Western Australia. Davoodian et al. (2020b) inferred 1002 ITS operational taxonomic units for the Boletales across Australia; assuming the diversity of Australian Boletales is between half this number and 1000 species, describing all Australian Boletales is a potentially achievable project with large teams of workers. By using environmental metagenomics to acquire rough estimates of species diversity throughout an area, in combination with graphing species accumulation curves at various scales, the discovery and eventual description of all species of *Gyroporus* and other Boletales traditionally described from fleshy basidiomes can be readily implemented across the globe.

New species publication rate

Given advances in phylogenetic systematic techniques, in recent years there has been major activity around describing new species of *Gyroporus*, which has aided in untangling the species complexes and expanded the occurrence of novel described species to Australia as well as South America (e.g. Davoodian et al. 2018, 2019, 2020a; Magnago et al.

2018a, b; Table 4; Fig. 4). Based on the phylogenetic and morphological diversity uncovered in these and other recent studies, the number of species of *Gyroporus* is likely to be in the range of 70–100. East Asia and Southeast Asia especially appear to be the largest reservoir of undescribed *Gyroporus* diversity (Davoodian et al. 2018, 2020a).

TRICHOLOMA

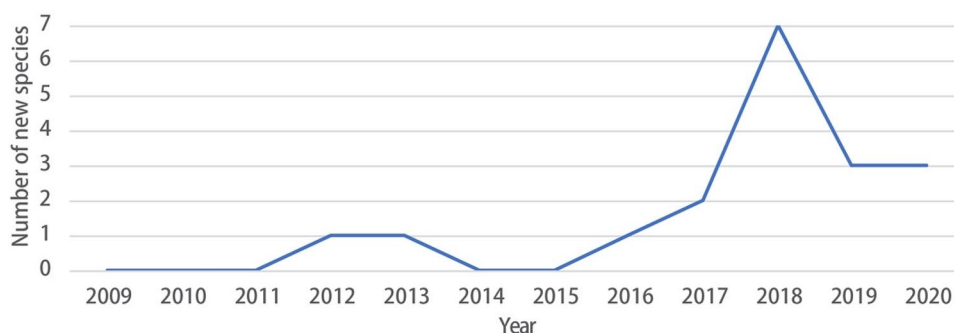
Tricholoma was established as a tribus within the genus *Agaricus* (Fries 1821) and then erected as a distinct genus by Staude (1857). *Tricholoma* now is the type and largest genus of the conserved family *Tricholomataceae* (McNeill et al. 2006) as recently circumscribed by Sánchez-García et al. (2014) using molecular data. Over the years more than 1000 names (including species and infraspecific taxa; 1293 according to Index Fungorum, <http://www.indexfungorum.org/>, accessed on 27 Oct. 2020; 1350 according to Mycobank, <https://www.mycobank.org/>, accessed on 27 Oct. 2020, Robert et al. 1999; 1104 according to Catalogue of Life, Roskov et al. 2020) have been published or combined in the genus and many of these have since been transferred to other genera, based on morphological and/or molecular data (Singer 1986; Trudell 2012; Christensen and Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017; Reschke et al. 2018). Currently, about 250 species are recognized in *Tricholoma* s. s. worldwide (Kirk et al. 2008; Ovrebo and Hughes 2018; Reschke et al. 2018; He et al. 2019; Ovrebo et al. 2019; Xu et al. 2020). This genus diverged from its saprotrophic sister genera *Dermoloma* and *Pseudotracholoma* and began diversification during the late Eocene, 61 (36–92) Mya, possibly with *Pinaceae* as ectomycorrhizal hosts (Sánchez-García 2016; Sánchez-García and Matheny 2017), favored by cooling temperatures and the expansion

Table 4 Number of new *Gyroporus* species published per year between 2009 and 2020

Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number	0	0	0	1	1	0	0	1	2	7	3	3

New species publication rate 0.150 (18/10/12)

Fig. 4 Line chart of new *Gyroporus* species described per year between 2009 and 2020



of their host communities, as shown in other groups of ECM fungi (Ryberg and Matheny 2012; Looney et al. 2016; Sánchez-García 2016; Sánchez-García and Matheny 2017; Sato and Toju 2019).

Tricholoma has been restricted to species with centrally stipitate, fleshy fruitbodies with adnate-sinuate lamellae (tricholomatoid habit), white spore-print and smooth, hyaline, inamyloid spores (Gulden 1969; Bon 1984, 1991; Singer 1986; Shanks 1997; Bessette et al. 2013; Christensen and Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017; Reschke et al. 2018). Vizzini et al. (2020), using a novel standardized method to test sporal amyloidity showed evidence that in the tested European species of this genus, the spores are amyloid. *Tricholoma* is widely accepted or supposed to be an ectomycorrhizal (ECM) genus (Trappe 1962; Garrido 1988; Molina et al. 1998; De Roman et al. 2005; Agerer 1999, 2006; Zeller et al. 2007; Rinaldi et al. 2008; Teder-soo et al. 2010; Ryberg and Matheny 2011; Christensen and Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017). However, the genus also encompasses some species that form dual ectomycorrhizal/monotropoid or ectomycorrhizal/pyroloid associations linking trees and monotropoid or pyroloids mycoheterotrophic plants (Ericaceae) (Björkman 1960; Bidartondo and Bruns 2001, 2002; Leake et al. 2004; Bidartondo 2005; Teder-soo et al. 2007; Trudell 2012) or are associated with green or achlorophyllous orchids (Jacquemyn et al. 2016; Pecoraro et al. 2018; Schweiger 2018; Chen et al. 2019b). *Tricholoma matsutake* was suspected to be parasitic on pine roots without forming a fungal mantle (mycoclena) or a Hartig net (Masui 1927; Ogawa 1975; Yamanaka et al. 2020). Yamada et al. (1999a, b), Guerin-Laguette et al. (2004) and Endo et al. (2015), however, demonstrated that *T. matsutake* form on roots of seedlings, in field and in vitro, true ectomycorrhizae with a fungal mantle and a well-developed Hartig net. *Tricholoma matsutake* can also behave as a root endophyte of arbuscular mycorrhizal trees (Murata et al. 2013, 2014; Selosse et al. 2018). *Tricholoma* species form medium-distance exploration types with uniformly shaped or differentiated rhizomorphs (Agerer 1999, 2006).

Species diversity of *Tricholoma*

Tricholoma species show a worldwide distribution (Teder-soo et al. 2010; Christensen and Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017; Reschke et al. 2018), but they seem to be the most common and diverse in temperate and subtropical zones in both the southern and northern hemisphere. The host plants are mainly trees belonging to *Pinaceae*, *Fagaceae*, *Betulaceae* and *Salicaceae* (Trudell 2012; Bessette et al. 2013; Christensen and Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017; Reschke et al. 2018) but some *Tricholoma* species are associated with

Eucalyptus (*Myrtaceae*) (Bougher 1996), *Dryas* (*Rosaceae*) and *Helianthemum* (*Cistaceae*) (Christensen and Heilmann-Clausen 2013), *Ericaceae* (subfamilies *Monotropeae* and *Pyroloideae*) (Leake et al. 2004; Bidartondo 2005; Teder-soo et al. 2007; Trudell 2012) and *Orchidaceae* (Jacquemyn et al. 2016). Some species prefer to fruitify in old and rather unmanaged forests (Christensen and Heilmann-Clausen 2013; Dvořák et al. 2017) and can be used as indicators of natural forests.

The diversity hotspot of *Tricholoma* species appears to be the North American area, for which more than 100 accepted species have been reported (Trudell 2012; Bessette et al. 2013; Trudell et al. 2017; Ovrebø and Hughes 2018; Reschke et al. 2018). Sixty-three to 88 species are listed from Europe (Bon 1984, 1991; Riva 1988, 1998, 2003; Galli 2005; Kirby 2012; Christensen and Heilmann-Clausen 2013). Fifty-five species are reported from Turkey (Intini et al. 2003, 2015; Sesli and Denchev 2008; Doğan and Akata 2011; Vizzini et al. 2015; Şen et al. 2018; Şen and Alli 2019; Haelewaters et al. 2020). About 50 species have been reported from China (Deng et al. 2004; Deng and Yao 2005; Yu et al. 2006; Hosen et al. 2016; Yang et al. 2017; Reschke et al. 2018; Xu et al. 2020). From other Asian areas, there are scattered reports from Japan (Kawamura 1954; Hongo 1959, 1968, 1974, 1983, 1988, 1991; Imazeki et al. 1988), Korea (Murata et al. 2008; Park et al. 2014), Vietnam (Kiet 1998), Laos (Wan et al. 2012), Thailand (Sanmee et al. 2007), Malaysia (Corner 1994, who used a very broad *Tricholoma* genus concept), Bhutan (Wan et al. 2012), India (Tanti et al. 2011; Gogoi and Sarma 2012; Khaund and Joshi 2013) and Nepal (Adhikari 2014). Reports from other parts of the world are those from Australia (Bougher 1996) and New Zealand (Stevenson 1964; Orlovich and Cairney 2004), North Africa (Maire 1915; Malençon and Bertault 1975; Kytövuori 1988; Ota et al. 2012; Benazza-Bouregba et al. 2016), Central America (Costa Rica, Ovrebø et al. 2019) and South America (Horak 1964; Singer 1954, 1966).

Several *Tricholoma* species seem to have a circumboreal distribution in Asia, Europe and North America: e.g. *T. albobrunneum*, *T. cingulatum*, *T. matsutake*, *T. roseoacervum*, *T. vaccinum* (Heilmann-Clausen et al. 2017; Trudell et al. 2017; Reschke et al. 2018). Some species (~20%, Sánchez-García 2016; Sánchez-García and Matheny 2017) show an extreme host specificity and may be restricted to a single host genus or species, such as *T. diemii* and *T. patagonicum* with *Nothofagus dombeyi*, *T. albobrunneum* and *T. imbricatum* with *Pinus* spp., *T. cingulatum* with *Salix* spp., *T. populinum* with *Populus* spp., *T. dulciolens* and *T. inamoenum* with *Picea* spp., *T. quercetorum* with *Quercus* spp. (Singer 1954; Grubisha et al. 2012; Christensen and Heilmann-Clausen 2013; Reschke et al. 2018); many other species such as *T. argyraceum*, *T. sculpturatum*, and *T. sulphureum* are reported in association with various hosts (Bon 1984, 1991;

Riva 1988, 2003; Molina et al. 1998; Galli 2005; Carriconde et al. 2008; Jargeat et al. 2010; Christensen and Heilmann-Clausen 2013; Sánchez-García and Matheny 2017; Reschke et al. 2018).

Species identification and section recognition within *Tricholoma* traditionally relied on morphological features such as pileus colour, structure of the pileipellis, presence/absence of clamp-connections, presence/absence of hymenial cystidia, size and shape of the basidiospores (Bon 1984, 1991; Singer 1986; Riva 1988, 1998, 2003; Shanks 1997; Kirby 2012; Trudell 2012; Bessette et al. 2013; Christensen and Heilmann-Clausen 2013). Such morphological delimiting characters were supported as useful and phylogenetically informative by molecular analyses (e.g., Heilmann-Clausen et al. 2017; Reschke et al. 2018). The nrITS region is still the most widely used molecular marker in species delimitation within *Tricholoma* and it has been found to be a suitable barcode (Comandini et al. 2004; Carriconde et al. 2008; Mouhamadou et al. 2008; Jargeat et al. 2010; Heilmann-Clausen et al. 2017; Trudell et al. 2017; Reschke et al. 2018; Ovrebo et al. 2019; Xu et al. 2020), but see the caveats in Badotti et al. (2017). Other markers, such as the V6 and V9 domains of the mitochondrial SSU-rDNA (Mouhamadou et al. 2008), the 5' part of the mitochondrial *cox1* gene (Moukha et al. 2013), the *gpd* gene (Jargeat et al. 2010; Ota et al. 2012), megB1 region (Ota et al. 2012) and the *tef* gene (Jargeat et al. 2010; Ota et al. 2012) were used coupled or not to nrITS. In particular, sections *Genuina*, *Caligata*, *Contextocutis*, *Sericella*, *Terrea* and *Tricholoma* are in urgent need of further phylogenetic studies because *T. equestre* s.l., *T. sulphureum* s.l., *T. viridilutescens/sejunctum*, *T. caligatum* group, and *T. scalpturatum/argyraceum* are species complexes showing considerable cryptic diversity (Kytövuori 1988; Kalamees 2001; Carriconde et al. 2008; Jargeat et al. 2010; Moukha et al. 2013; Heilmann-Clausen et al. 2017; Trudell et al. 2017; Reschke et al. 2018).

The knowledge of the diversity and distribution of *Tricholoma* species on a global scale is generally still unsatisfactory and patchy. Species diversity of *Tricholoma* species appears quite well-studied in Europe (above all in the north-western part), and important recent monographic works in Europe are those of Gulden (1969), Bon (1984, 1991), Riva (1988, 1998, 2003), Noordeloos and Christensen (1999), Galli (2005), Christensen and Heilmann-Clausen 2008, 2012, 2013; Kirby 2012 and Heilmann-Clausen et al. (2017). Heilmann-Clausen et al. (2017) provided the first comprehensive molecular analysis (only ITS based) of the genus, focused on northern European species. Molecular works focused only on sections or species complexes are those by Carriconde et al. (2008), Mouhamadou et al. (2008), Moukha et al. (2013), Jargeat et al. (2010). Reschke et al. (2018) is the first molecular analysis combining *Tricholoma* collections from Europe, North America and Asia.

An estimate of total fungal diversity in Europe based on the ideal 6:1 ratio of fungi/vascular plants proposed by Hawksworth (1991, 2001) would suggest that, in general, the fungal diversity in Europe is well investigated (over 75,000 fungal species/over 12,500 plant species, 6:1 ratio, Senn-Irlet et al. 2007).

Despite being the area for which the highest number of species (100) has currently been surveyed, in North America the genus *Tricholoma* historically has received relatively little attention. Compared to the situation in Europe, North American *Tricholoma* species are poorly known and nearly all groups/sections are in need of additional study (Trudell 2012; Reschke et al. 2018). The over 60 *Tricholoma* species described by Peck in the late 1800s and early 1900s (e.g., Peck 1875, 1891, 1900, 1904, 1912), and those described by Murrill in the first half of the 1900's (e.g., Murrill 1913, 1938, 1942, 1945, 1949) are still difficult to interpret and many of them were later transferred to other genera. The studies by Kauffman (1918), Smith (1942), Hesler (1958) and Bigelow (1979) were not carried out in a monographic perspective. Then, the most important contributions were those by Ovrebo (1973, 1980, 1986, 1989), Ovrebo and Tylutki (1975), Ovrebo and Smith (1979), Ovrebo and Hughes (2018), mainly focused on Pacific Northwest and the Great Lakes region and often interpreting some of Peck's species concepts; by Shanks (1994, 1996, 1997) mainly on *Tricholoma* species from California; Bessette et al. (2013), with the first comprehensive monograph on North American *Tricholoma* spp.; Trudell et al. (2017), Ovrebo and Hughes 2018 and Reschke et al. (2018) using molecular markers. Additional studies are needed to deepen the knowledge concerning the diversity and taxonomy of *Tricholoma* spp. in North America. Bates et al. (2018) reported for North America a 1.9:1 ratio (44,000 fungal species/23,000 plants).

China, albeit with only 50 species listed, is the Asian area with the greatest diversity of *Tricholoma* species (Deng et al. 2004; Deng and Yao 2005; Yu et al. 2006; Hosen et al. 2016; Yang et al. 2017; Reschke et al. 2018; Xu et al. 2020). Scarce and scattered is the knowledge about the presence of *Tricholoma* species in adjacent Asian countries due to the lack of modern comprehensive treatments (Reschke et al. 2018). The knowledge of *Tricholoma* in China is still limited, as relatively few studies have been devoted to this topic. Deng et al. (2004) provided an annotated checklist of *Tricholoma* from China (40 species) and Deng and Yao (2005) made revision of some *Tricholoma* species reported from China. Since then, 12 new species were described from China (Yu et al. 2006; Hosen et al. 2016; Yang et al. 2017; Reschke et al. 2018; Xu et al. 2020). As one of 17 megadiverse countries (Noss 1990), China is a hotspot extremely rich in biodiversity and endemism, and its Flora consists of about 35,000 plant species (Ministry of Environmental Protection of China (EMP), 2011; Volis 2018), while, on the

contrary, the database for the Checklist of Fungi in China currently contains around 27,900 fungal species (Fang et al. 2018; Institute of Microbiology, Chinese Academy of Sciences 2018), with a 0.8:1 ratio. Focusing on a smaller area, Northern Yunnan in southwest China is part of one of the 25 world biodiversity hotspots of the world (Myers et al. 2000). About 15,000 seed plant species and 7,000 fungal species are reported from Yunnan (Yang et al. 2004), which leads to a 0.46/1 ratio (7000/15,000), a ratio very far from the ideal 6:1 ratio proposed by Hawksworth (1991, 2001) (but see also Tedersoo et al. 2014 and Hawksworth and Lücking 2017 for a reassessment of diversity ratios).

The 250 *Tricholoma* species so far recognized worldwide are an underrepresentation of the actual biodiversity of the genus. Cryptic speciation occurrence revealed in some *Tricholoma* species by molecular analyses (e.g. Carriconde et al. 2008; Jargeat et al. 2010; Heilmann-Clausen et al. 2017; Yang et al. 2017) does not facilitate the assessment of specific diversity (Hawksworth and Rossman 1997; Hawksworth and Lücking 2017). Based on studies of selected fungal complexes available, it was suggested that, in general, the number of known fungi might rise by a factor of five (Hawksworth and Rossman 1997) or more (up to eleven according to Hawksworth and Lücking 2017) for cryptic speciation. The application of multiple genetic markers will allow to untangle the species complexes.

The status of many species described from North America is unclear. The application of taxa originally described from Europe on American specimens must be redefined for many species. As said by Trudell (2012), “For now, a bigger issue comes from not knowing whether the North American fungi to which European names have been applied really do belong to the same species. Few, if any, mycologists have spent enough time on both continents to have firsthand comparative knowledge of large numbers of their respective fungi and few critical studies have been done to evaluate our use of European names.

The number of *Tricholoma* species recorded in North America and Asia is scarce compared to those in Europe, considering the extension of these geographical areas and the fact that in Asia and America there is the greatest diversity of *Pinaceae* and *Fagaceae* (the two most important host families for *Tricholoma* species) at genus and species level (Nixon 2006; Kremer et al. 2007; Eckenwalder 2009; Cannon et al. 2018; Farjon 2018). Most *Tricholoma* species are able to form ECM associations with a wide range of host trees, and, probably, this generalist attitude may have allowed them to explore and adapt to new environmental niches, and consequently increasing their rate of diversification (Sánchez-García 2016; Sánchez-García and Matheny 2017). As it was generally pointed out by Tedersoo et al. (2014), ectomycorrhizal species richness is strongly related to the richness of host plant species.

Further research is needed to increase the knowledge concerning the taxonomy, diversity and phylogeography of *Tricholoma* species worldwide. A careful sampling strategy of North American and Asian areas will be crucial, but also Australia, New Zealand and South America should be included. Biodiversity analyses will also have to take into account the ongoing outputs from the metabarcoding methods (Tedersoo et al. 2014; Hawksworth and Lücking 2017; Khan et al. 2020).

New species publication rate

The number of described fungal species accelerated in the last decade (2009–2020) after the advent of molecular approaches to species delimitation (Hawksworth and Lücking 2017). Apart from some intraspecific taxa [e.g., *T. sulphureum* var. *nigrescens* (Gillet) Deparis (Deparis 2013, *T. virgatum* var. *fulvoumbonatum* Sesli, Contu and Vizzini (Vizzini et al. 2015), *T. sulphureum* var. *inolens* Chiarello & Battistin (Chiarello and Battistin 2018), *T. viridifucatum* var. *etruriae* Raumi, Martolini, Matteini and Pierotti (Raumi

Table 5 Number of new *Tricholoma* species published between 2009 and 2020

Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number	2	1	1	1	1	0	1	2	6	7	3	7

New species publication rate 0.0133 (32/200/12)

Fig. 5 Line chart of the number of new *Tricholoma* species published from 2009 to 2020

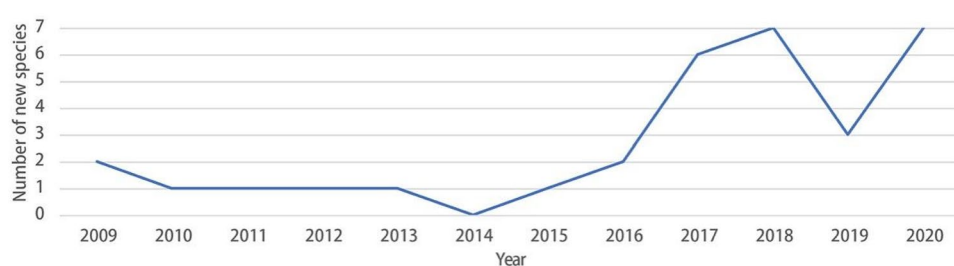


Fig. 6 European *Russula* described in the past two centuries (1793–2003) by European mycologists with indication of the most important published genus monographs or other major contributions by professional (in red) and amateur (in green) mycologists

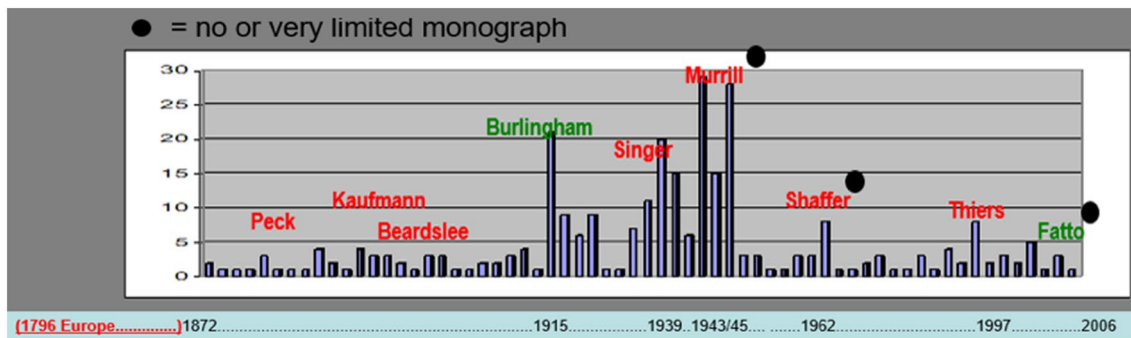
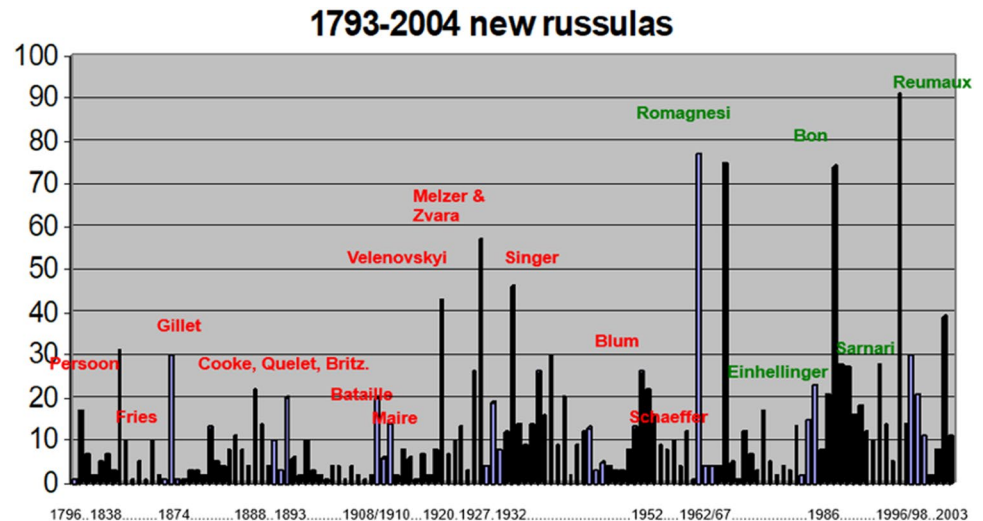


Fig. 7 American *Russula* described in the past two centuries (1872–2006) by American mycologists with indication of the most important published genus monographs or other major contributions by professional (in red) and amateur (in green) mycologists

et al. 2019)], a *nom. inval.*, *T. grave* (Bessette et al. 2013) and four *nomina nova* published by Blanco-Dios (2020) for replacing four Malaysian taxa whose names are preoccupied (Corner 1994), 26 new species were established between 2010 and 2020 (see Table 5), constituting 10% of the species currently recognized in *Tricholoma* (about 250, Kirk et al. 2008; Ovrebo and Hughes 2018; Reschke et al. 2018; He et al. 2019; Ovrebo et al. 2019; Xu et al. 2020). Eleven were described from Asia (China), eight from Europe, three from Central America (Costa Rica), two from Turkey, and two from North America (USA and Mexico); 20 of which have been described in the last 4 years (Fig. 5).

RUSSULA

Russula is the type genus of the russuloid clade or the order Russulales, and the ancestor of Russulales diverged during late Jurassic (170–180 Mya) (Zhao et al. 2017a, b; Varga et al. 2019). In taxonomic study, it is a very old genus, dating back to the end of the eighteenth century (Persoon 1796),

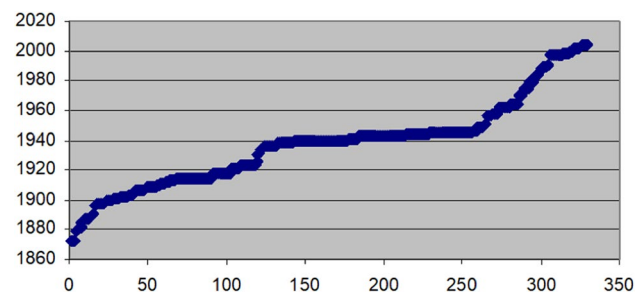


Fig. 8 Species number of *Russula* from 1860 to 2005 (416 species in total including 329 species from USA and 87 species from Europe)

probably because it is so prominently present in most habitats, so extremely diverse and also very well characterizable both in the field and under the microscope. Consequently, it has attracted the interest of many professional and amateur mycologists and is undoubtedly one of the most frequently monographed genera of larger mushrooms (see Fig. 6).

Most of the traditional complex infrageneric classification of the genus has been laid out in these European monographs, especially those written in more recent years by eminent amateur mycologists (Romagnesi 1967, 1987; Sarnari 1998, 2005; Bon 1988). In Europe, this amateur community represents in Europe the major source of expertise in the genus since the 1960s.

In other parts of the world, the diversity of the genus has been largely neglected as was the case for most of the other macrofungi, with two notable exceptions though: The United States of America and Central Africa. The exploration and description of the existing *Russula* diversity in North America started approximately a century later compared to Europe (see Figs. 7, 8), essentially with the studies of Peck (see Adamčík et al. 2018). However, the clear gap between professional and amateur mycologists in America was responsible for the sudden arrest of local *Russula* research once the professional expertise had vanished, leaving this continent at the beginning of the twenty-first century with an astonishing number of 329 different endemic *Russula* that had been described (in addition to an estimated number of 87 European *Russula* that had been reported from the area) but that quasi nobody in America was able to identify any more.

The second part of the world for which *Russula* diversity was fairly well-documented during the past century is tropical Africa (including Madagascar), where the mycological exploration of larger mushrooms had its roots in the colonial period. For *Russula*, apart from many smaller contributions, the principal monographs were those published in the Fungus flora of Central Africa series (<https://www.ffa-online.org/>) by Buyck (1993, 1994, 1997) and in the “Prodrôme a une flore mycologique pour Madagascar et Dépendances” series by Heim (1938), culminating in almost 200 hundred different, well-illustrated and described *Russula* species and their infraspecific taxa for tropical Africa at the beginning of the twenty-first century.

Species diversity of *Russula*

Russula has always been considered one of the most diverse ectomycorrhizal mushroom genera, whereas older handbooks estimated the total number of *Russula* species in the world to be around 700–800 (Kirk et al. 2008), the most recent estimates are higher. Looney et al. (2016) calculated that the number of sequenced OTUs in the northern hemisphere was already in excess of 1000, but Buyck (2012) estimated on the basis of more than 10 years of collecting in North America that the number of North American *Russula* alone was surely closer to 1500 than to the ca. 450 known at present. The total number of *Russula* species in the world has been estimated to be in excess of 3000 (He et al. 2019), but could still be higher. These high estimates seem at least supported by the fact that many newly published *Russula*

species are not known from environmental sequences, while most of the continents are largely unexplored with exception of Europe and, to a lesser degree, also North America. Indeed, unpublished results from inventories in little or unexplored parts of the world such as Madagascar and New Caledonia show that probably their entire *Russula* mycota may be original as even morphologically similar species are genetically distant from their closest relatives.

New species publication rate

During the past ten years the situation has changed profoundly, and this time on all continents. The main game changer has been the development of molecular tools at the end of the twentieth century and their impact on species descriptions and fungal phylogenies. Even for beginners, *Russula* was always a very ‘easy’ genus to recognize in the field, at least in Europe, but the genus was reputed extremely difficult as to the recognition of the various individual species because of the often-incredible variation in color and other features, and this notwithstanding a rich array of microscopic features compared to many other mushroom genera. This morphological variability ultimately led to an exaggerated multiplication of names at different nomenclatural ranks (species, variety or form) given to the same taxa by different mycologists.

During the past decennium, the number of new *Russula* species published each year oscillated between 10 and 15, except for a few years when new species numbers skyrocketed. In 2011, for example, there were 88 new *Russula* taxa published, 23 new species and many new varieties and forms, all of them uniquely based on often rather insignificant morphological differences. The large majority of these new taxa were described in a new *Russula* monography published in Eastern Europe (Socha et al. 2011), others were described by a French *Russula* expert with a prolific record of new species and infraspecific taxa (Freund and Reumaux 2011). The year 2011 therefore resembles other years in the past (e.g. Reumaux et al. 1996; Reumaux and Moenne-Lozcz 2003) when similar monographs were published with many new species and infraspecific taxa entirely based on subjective interpretations of sometimes minor morphological differences. Nowadays, large monographic works that introduce large numbers of new species in *Russula* purely based on morphology are becoming increasingly rare in the modern era of sequence data. Indeed, with the introduction of ITS barcode sequences to characterize species most of the subjectivity in species recognition shifted from morphology to interpretation of nucleotide differences (Li et al. 2019a, b), especially since most new species are now often described by young mycologists with hardly any experience with morphological recognition of *Russula* species.

More recently, there has been another sudden surge in novel *Russula* names with the publication in 2017, 2018 and 2019 of respectively 78, 115 and 42 new *Russula* species. This time, the explanation is entirely different from the one in 2011 as no monograph or other major revision is the origin of this avalanche of new names, but rather a purely technical implication of previously published phylogenetic results. Indeed, similarly to many other lineages of agaricoid mushrooms, earlier molecular phylogenies (e.g. Miller et al. 2001; Lebel and Tonkin 2007) had suggested that several secotiid to entirely hypogeous genera in Russulales were possibly synonymous with older agaricoid genera, representing convergent evolutions toward similar morphologies in unrelated terminal clades. The publication of new species of ‘truffle-like’ *Russula* had started with a paper by Lebel and Tonkin (2007) describing several novel species from Australia supported by molecular sequence data. Massive recombination of the known species of these secotiid to hypogeous relatives into *Russula* followed only recently with papers published by Lebel (2017) and Elliot and Trappe (2018) (Table 6; Fig. 9).

CANTHARELLUS

Cantharellus, is the type genus of the cantharelloid clade or the order Cantharellales. The ancestor of *Cantharellus* occurred around late Jurassic (170–180 Mya) or earlier (280 Mya) (Zhao et al. 2017a, b; Varga et al. 2019). In taxonomy study, it is a very old genus and the first published mention of the name ‘Cantharel’ date back to the mid-eighteenth century (Adanson 1763). The genus delimitation and systematic placement of *Cantharellus* has a very turbulent history (Buyck et al. 2014), most likely due to the very poor diversity of useful microscopic features for species recognition

and the very similar overall morphology shared with many other mushroom genera. Of the 346 species described in *Cantharellus* at the end of the twentieth century, the genus-wide type revisions by Eyssartier (2001) demonstrated that only 59 species were good members of *Cantharellus*; all other names had been recombined in as many as 40 different genera distributed over nine of the major clades in Agaricomycetes (Buyck et al. 2014).

Modern phylogenies have demonstrated that *Cantharellus* belongs to one of the oldest mushroom-forming clades in Basidiomycota (Zhao et al. 2017a, b). This might explain the poor diversity of microscopic features (no spore ornamentations, lack of well-differentiated cystidia in any of their tissues) and the important variation in some of these, such as the instability of the number of spores produced per basidium, or the absence or presence of clamp connections among infrageneric clades. It is therefore not surprising that phylogenetic analyses of sequence data have profoundly impacted species recognition that was, before the advent of molecular tools, primarily based on field habit. Also, a correct genus delimitation, in particular from its sister genus *Craterellus*, was only possible after the introduction of molecular data (Feibelman et al. 1994; Dahlman et al. 2000). Today, species recognition in *Cantharellus* has primarily become a matter of sequence data, although successful sequencing of the typical fungal barcode (nr ITS) poses major problems because of its unusual length (up to > 1500 base pairs) and extreme variability, favoring the use of *tef-1* sequences to characterize species (Buyck and Hofstetter 2011).

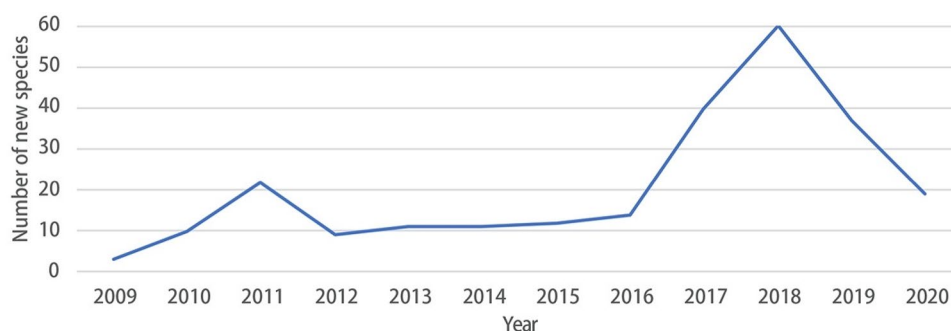
Species diversity of *Cantharellus*

Contrary to many other ectomycorrhizal genera, such as *Russula*, which are common in appropriate habitats on all continents, the existing biodiversity of *Cantharellus* varies

Table 6 Number of new *Russula* species published per year between 2009 and 2020

Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number	3	10	22	9	11	11	12	14	40	60	37	19
New species publication rate	0.0276 (248/750/12)											

Fig. 9 Line chart of number of new *Russula* species published from 2009 to 2020



greatly between continents (Buyck 2016) and reflects most likely its different evolutionary history. Indeed, whereas lower diversity in Europe may probably be explained by recent glaciations, both South America and Australia seem extremely poor in *Cantharellus* species, with only a handful of species known from either continent. This is in great contrast with the extreme biodiversity of *Cantharellus* in tropical Africa (including Madagascar), with already more than 90 different species, and the steadily growing number of chanterelles that are described from North America and Asia. Future biogeographic interpretations based on broadly sampled, multi-marker phylogenies will hopefully offer an appropriate explanation for the distribution pattern of *Cantharellus*.

New species publication rate

During the past 10 years the number of new *Cantharellus* species has been constantly growing at a rate of five to 15 new species published every year, or a total of 90 new species between 2010 and 2020. Compared to the 19 new *Cantharellus* species published between 2000 and 2009 (this number does not account for infra-specific or infra-generic taxa, nor for two species that have since been transferred to *Craterellus*), this is a considerable progress, putting the total number of accepted *Cantharellus* species now at 166 or almost three times more than there were 20 years ago. The publication rate of new species is not expected to diminish in the years to come as many undescribed taxa await description, particularly in Africa and Asia (Buyck 2016), justifying a total biodiversity estimate for *Cantharellus* ranging from 250 to perhaps 300 species worldwide (Table 7, Fig. 10).

Plant parasitic basidiomycetes

RUST FUNGI

Rust fungi (Pucciniales) are amongst the most collected and studied fungi, in part due to their impact to agriculture as well as distinctive disease symptoms. Rust fungi are obligate biotrophic pathogens of plants and the largest pathogenic order in the Basidiomycota (Cummins and Hiratsuka 2003). Rust fungi are highly host-specific, yet their evolution has been driven by host jumps to unrelated plants, followed by adaptive radiation and switches to proximal hosts (van der Merwe et al. 2008; McTaggart et al. 2016; Aime et al. 2018a; Aime and McTaggart 2021). The phenotypic

and genetic diversity of rust fungi is reflected across seven suborders and 18 families (Aime and McTaggart 2021).

The starting point for binomial names of rust fungi is *Synopsis Methodica Fungorum* (Persoon 1801). By the height of the Agricultural Revolution in the 1850s, more than 1500 rust fungi had been named and described, mostly from Europe and North America. Up to the end of the twentieth century, revisionary studies of rust fungi were based on morphology (Sydow and Sydow 1904, 1915) and/or host range (Cummins 1937, 1940a, b, 1943a, b, 1945). Notable regional revisions of rust fungi have been composed for Australia (McAlpine 1906), Europe (Sydow and Sydow 1904, 1915; Dietel 1928), Japan (Hiratsuka et al. 1992), New Zealand (Cunningham 1931), North America (Arthur 1907–1931) and South Africa (Doidge 1950).

The largest radiation of rust fungi is found in the Pucciniaceae, whose members shared a most recent common ancestor between 15 and 65 Mya (McTaggart et al. 2016; Aime et al. 2018a; Aime and McTaggart 2021). The evolutionary success of the Pucciniaceae is evident by (i) their known diversity that accounts for almost half of all rust fungi, including almost 4000 species in *Puccinia*, (ii) their ability to infect diverse and unrelated hosts, and (iii) multiple pathways of evolution to convergent hosts (Dixon et al. 2010).

There are a few plant families that do not host rust fungi, notably the Dipterocarpaceae and Restionaceae. In Australia, two of the largest and most diverse plant families, Myrtaceae and Proteaceae, are hosts to very few rust fungi (Walker 1983), with exceptions in the Pucciniaceae, namely, *Puccinia cygnorum* (Shivas and Walker 1994) and *Uredo xanthostemonis* on Myrtaceae, and *Puccinia grevilleae* (McTaggart and Shivas 2008) and *Uredo angiosperma* on Proteaceae.

Species diversity of rust fungi

Approximately 320 genera of rust fungi have been described, of which ~125 generic names are in current use. Genera described before nomenclatural changes brought about by 1FIN were often based on a life cycle stage (asexual taxa), which did not indicate evolutionary relationships between taxa. Some examples of these asexual rust genera include *Campanulopsora*, *Canasta*, *Morispora* (Yepes et al. 2007), *Malupa* (Ono et al. 1992), *Petersonia* and *Wardia* (Cummins and Hiratsuka 2003). Seven of the nine genera described in the last decade are monotypic and from Asia, Australia or South America, namely *Austropuccinia* (Beenken 2017), *Caetea* (Yepes and de Carvalho 2012), *Crossospora*

Table 7 New species of *Cantharellus* published between 2009 and 2020

Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number	3	2	7	10	4	17	8	15	6	4	4	7

New species publication rate 0.1153 (87/65/12)

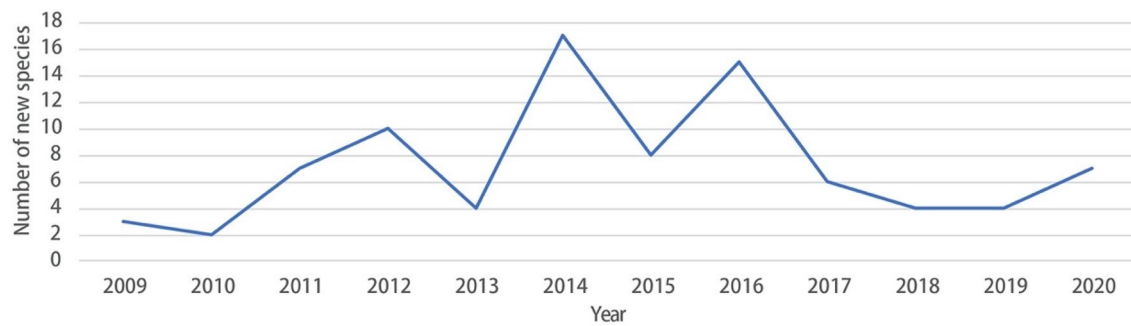


Fig. 10 Line chart of number of new *Cantharellus* species published from 2009 to 2020

(Souza et al. 2018), *Neopuccinia* (Junior et al. 2019), *Quasipucciniastrum* (Qi et al. 2019), *Puccorchidium* and *Sphenorchidium* (Beenken and Wood 2015). The two exceptions are *Neophysopella* with 13 species (Ji et al. 2019) and *Pelastoma* with two species (Yepes et al. 2012). Three challenges that currently face taxonomic resolution of rust fungi at

generic rank are (i) polyphyly of genera such as *Puccinia*, *Pucciniastrum* and *Ravenelia*, (ii) generic placement of species in asexual taxa, and (iii) taxonomic placement without comparison to types (Aime and McTaggart 2021).

There are approximately 10,559 accepted names of rust fungi at species rank (www.IndexFungorum.org, accessed

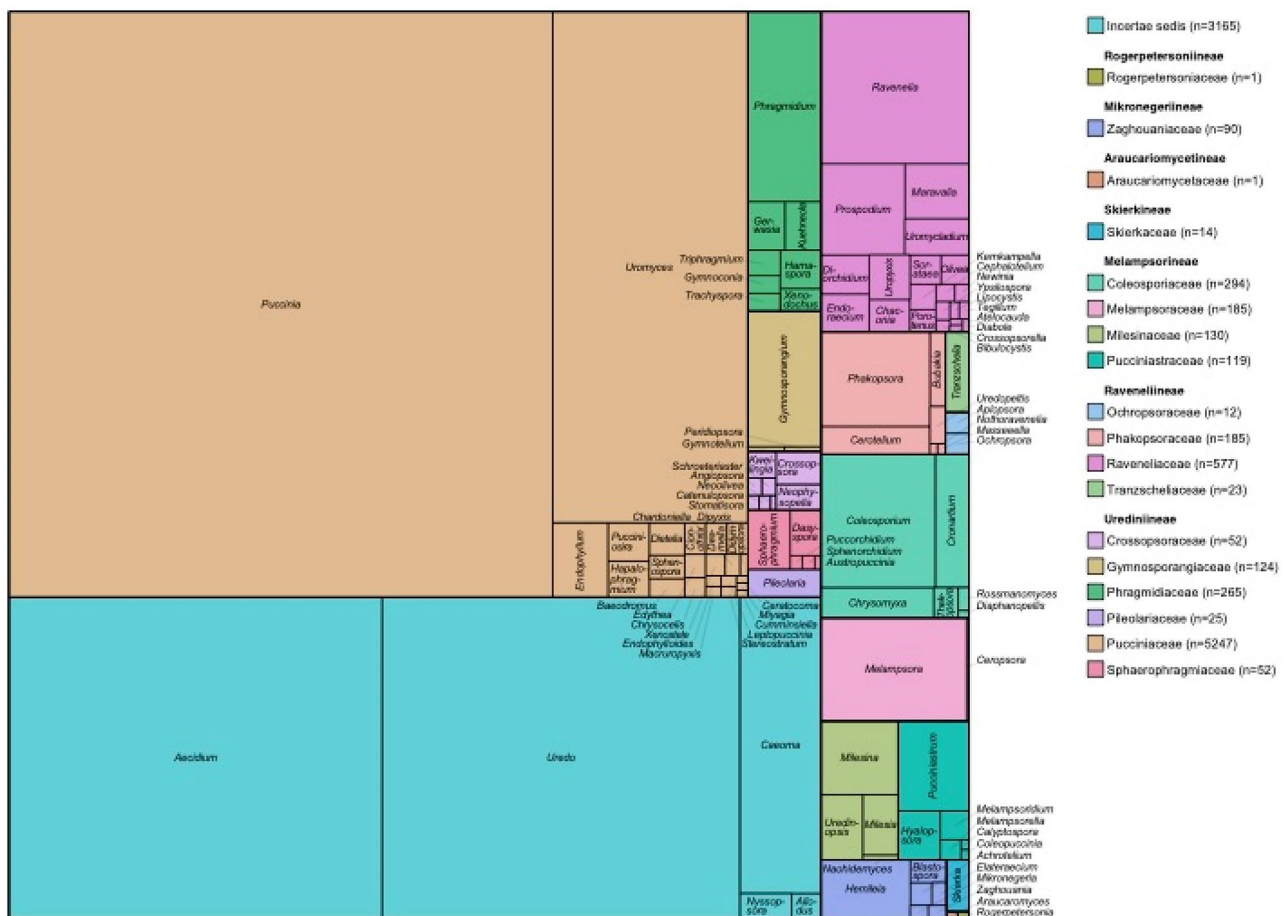


Fig. 11 Treemap of taxonomic placement at family and genus rank for 10,559 described species of rust fungi. Plotted using the Treemap package (Vitolo C. 2014. TreeMap, available at https://github.com/cvitolo/r_treemap) in R (R Core Team 2014)

9th Nov. 2020) (Fig. 11). This number was calculated by querying 110 generic names of rust fungi and excluding names that were variants below species rank as well as taxonomic or nomenclatural synonyms. The three most speciose genera, *Puccinia* (3978 species), *Aecidium* (1455 species) and *Uredo* (1394 species), are polyphyletic (Aime and McTaggart 2021).

New species of rust will certainly be found in isolated, under-explored, biodiverse areas, as well as through discovery of cryptic diversity in species complexes. For example, species diversity of rust fungi has increased through resolution of taxa in *Chrysomyxa* (Feau et al. 2011), *Coleosporium* (McTaggart and Aime 2018),

Dasyscypha (Beenken et al. 2012), *Endoraecium* (McTaggart et al. 2015), *Gymnosporangium* (Zhao et al. 2016a, b), *Melampsora* (Toome and Aime 2015; Zhao et al. 2017a), *Milesina* (Bubner et al. 2019), *Neophysopella* (Chatasiri and Ono 2008), *Phakopsora* (Beenken 2014; Maier et al. 2016), *Phragmidium* (Liu et al. 2018), *Puccinia* (Demers et al. 2017; Liu and Hambleton 2010, 2013), *Puccinias-trum* (Liang et al. 2006), *Ravenelia* (Ebinghaus and Bege-row 2018; Ebinghaus et al. 2018, 2020) and *Uromycladium* (Dounsa-ard et al. 2018) (Fig. 12).

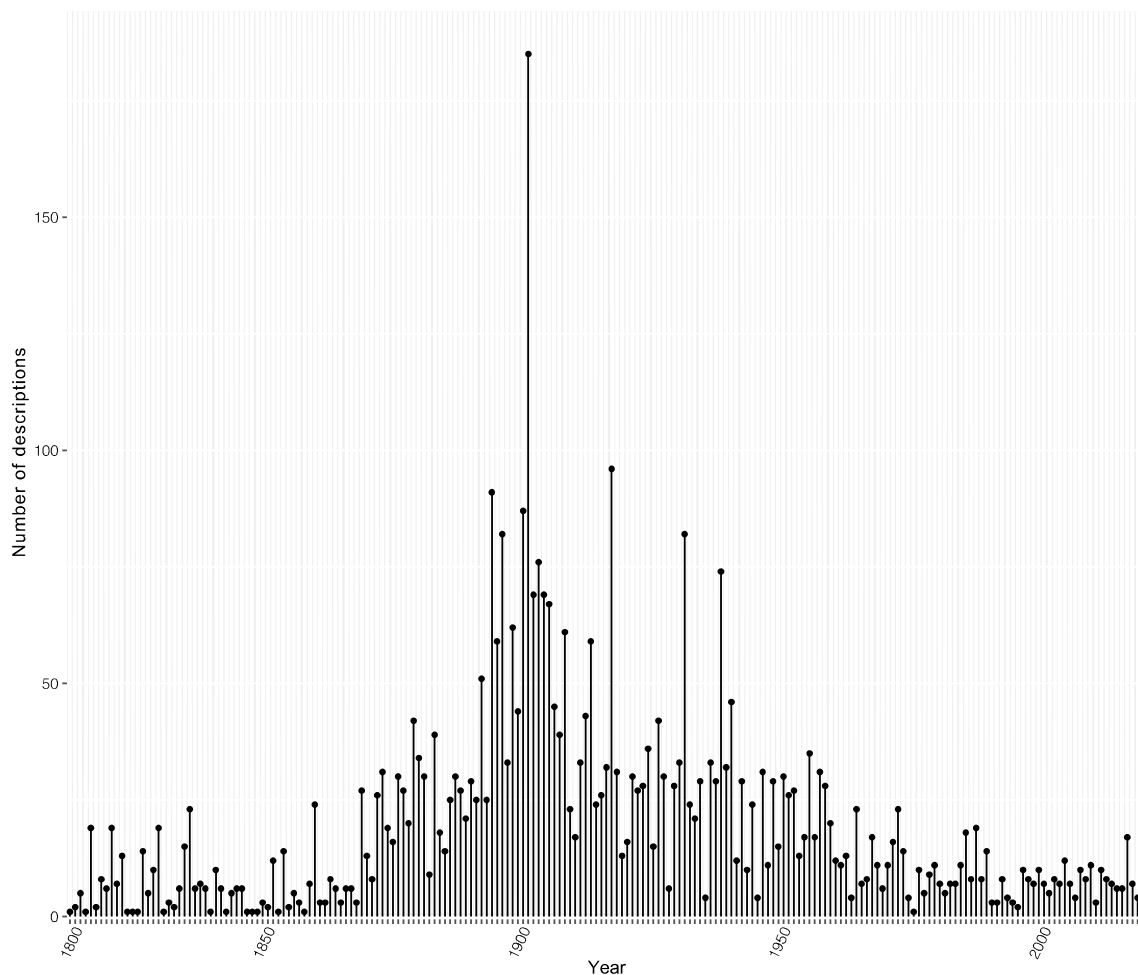


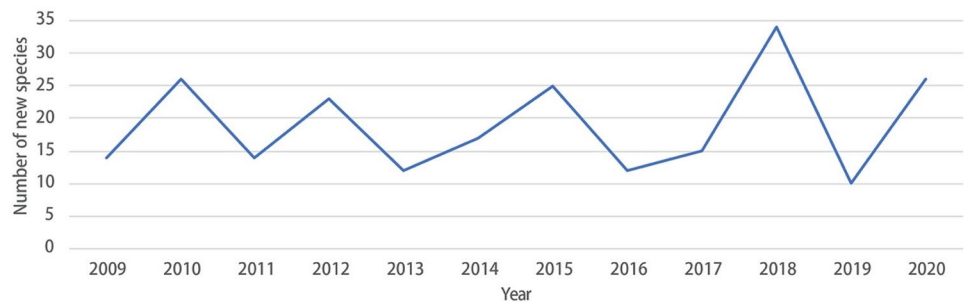
Fig. 12 Lollipop plot of the number of described species of *Puccinia* from 1800 to 2020. Made using ggplot (Wickham 2016) in R (R Core Team 2014)

Table 8 Number of new species of selected rust fungi published in between 2009 and 2020

Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number	14	26	14	23	12	17	25	12	15	34	10	26

New species publication rate 0.0029 (228/6570/12)

Fig. 13 Line chart of new species of selected rust fungi published from 2009 to 2020



New species publication rate

We searched *Mycobank.org* (Robert et al. 2013) to calculate the number of names described after 2009 in the largest genera of rust fungi based on Fig. 11, namely *Aecidium*, *Chrysomyxa*, *Dasyscypha*, *Endoraecium*, *Gymnosporangium*, *Melampsora*, *Milesina*, *Neophysopella*, *Phakopsora*, *Phragmidium*, *Puccinia*, *Pucciniastrum*, *Ravenelia*, *Uredo*, *Uromyces* and *Uromycladium* (Table 8; Fig. 13).

We predict that the rate of discovery of new taxa of rust fungi will decline in the future. The rigor with which rust fungi were collected in the golden age of mycological discovery (nineteenth and twentieth centuries) has declined. This is illustrated in Fig. 12 by the change in numbers of species of *Puccinia* described since 1801. Further, the rate of habitat loss bodes poorly for taxa that await discovery. We estimate that the number of extant rust fungi on this planet is ~ 10,000 species, which accounts for as yet unidentified taxonomic synonymy.

SMUT FUNGI

Classically, smut fungi are characterized by a specific life cycle that alternates between a dikaryotic, plant-parasitic stage and a haploid, saprobic yeast phase. The most characteristic trait of smut fungi is their thick-walled teliospores, which often results in a sooty-like appearance of affected plant parts. Only recently has it been realized that this group of fungi, which is very well-characterized by its life cycle, represents a phylogenetically, heterogeneous group that has evolved three times independently in Ustilaginomycotina, Microbotryales (Pucciniomycotina), and Entorrhizomycota (Begerow et al. 1997, 2014, 2018). Many taxa belonging to these clades do not exhibit the classical smut fungal lifestyle. In the Exobasidiomycetes (Ustilaginomycotina) deviations from the canonical smut fungal life cycle are often observed. *Exobasidium* species on Ericaceae or *Microstroma* species on various tree species, for instance, do not produce teliospores anymore, but produce basidia directly from their hyphae through the stomata of their hosts (e.g., Begerow et al. 2001, 2002). Additionally, phylogenetic studies have shown that many lineages that are exclusively known as

yeasts are found in these groups and it is assumed that several lineages have lost the ability to parasitize plants (Wang et al. 2015c; Kijpornyongpan et al. 2018; Nasr et al. 2019).

Several genera of smut fungi consist exclusively of species known only from their asexual states: *Acaromyces*, *Fereydounia*, *Golubevia*, *Jaminaea*, *Meira*, *Microbotryozyma*, *Moniliella*, *Quambalaria*, *Robbauera*, *Sympodiomyces*, *Tilletiopsis*, and *Violaceomyces*. Many yeasts were classified in large asexual genera, e.g. *Pseudozyma* (asexual Ustilaginaceae), *Rhodotorula* (asexual Microbotriales as well as a few Ustilaginales and Microstromatales species), and *Tilletiopsis* (asexual Exobasidiomycetes) until re-classification by Wang et al. (2015c, d). In *Microstroma*, *Mycosarcoma*, *Moesziomyces*, and *Ustilentyloma* it was possible to link independently discovered asexual and sexual states in several instances. The correct placement of asexual species into sexual genera is often hampered by the lack of sequences derived from teleomorphs. It is likely that sexual parasitic states of asexual species will be discovered among known fungal species when sequenced.

Species diversity of smut fungi

Over 2000 species of smut fungi and related lineages are currently known. By far the most species-rich are Ustilaginomycotina (1906 species), followed by Microbotryales (128), and Entorrhizomycota (18). Smut fungi are found mostly on herbaceous host plants, and some of the Exobasidiomycetes (e.g. *Exobasidium*, *Graphiola*, *Microstroma*, and *Quambalaria*) also occur on woody hosts. Smut fungi have been observed worldwide, including *Tilletia schenckiana* on *Deschampsia antarctica* from the Kerguelen Islands in the Antarctic region (Hennings 1906). The highest species diversity has been reported from the Northern Hemisphere, with most species in Europe and Asia. The available literature, monographs, and regional checklists suggest that these estimates of diversity are highly biased towards the northern Hemisphere, whereas other regions, especially in the tropics, are yet to be surveyed. The most comprehensive and still most up to date source concerning the diversity and distribution of smut fungi is the world monograph by Vánky (2011a).

Europe is the best studied continent (Vánky 1994), especially, Northern Europe (UK: Mordue and Ainsworth 1984; Norway: Jørstad 1963; Sweden: Lindeberg 1959; Nannfeldt 1979; Finland: Liro 1924, 1938; Denmark: Rostrup 1890), Central Europe (Belgium: Vanderweyden and Fraiture 2014; Germany: Scholz and Scholz 1988; Klenke and Scholler 2015; Austria: Zwetko and Blanz 2004; Switzerland: Zogg 1986; Poland: Kochman and Majewski 1973; Hungary: Vánky 1985), and the Carpathian Region (Vánky 1985). Monographs or checklists of smut fungi in Southwestern, Southern, and Southeastern Europe are published for France (Viennot-Bourgin 1956), Iberian Peninsula (Almaraz 2002), Italy (Ciferri 1938), Slovenia (Lutz and Vánky 2009), Croatia (Ivić et al. 2013), Romania (Săvulescu 1957; Vánky 1985), and Bulgaria (Denchev 2001), and for Eastern Europe: for the Baltic States (Ignatavičiūtė 1975, 2001), European Russia (Karatygin and Azbukina 1989; Azbukina and Karatygin 1995), and Ukraine (Savchenko and Heluta 2012). The distribution data for some of these countries are outdated while the information about the western and southern parts of the Balkan Peninsula and the Aegean Islands is lacking.

For Asia, monographs or checklists of smut fungi are published for Siberia and Russian Far East (Karatygin and Azbukina 1989; Govorova 1990; Azbukina and Karatygin 1995; Azbukina et al. 1995), Middle Asia (Uzbekistan: Ramazanov et al. 1987; and Kazakhstan: Schwarzman 1960), Transcaucasus (Azerbaijan: Ulyanishchev 1952), Western Asia (Israel: Savchenko et al. 2015; Iran: Vánky and Abbassi 2013), Indian Subcontinent (Ahmad et al. 1997; Vánky 2007), Central and Eastern Asia (Mongolia: Braun 1999; China: Guo 2000, 2011; Korean Peninsula: Denchev et al. 2007; Japan: Ito 1936; Kakishima 1982; Denchev et al. 2013a), Indo-China (Thailand: Shivas et al. 2007), and Papuaasia (Papua New Guinea: Shivas et al. 2001). Many regions in Siberia, Middle Asia, Caucasus, Western and Central Asia, Indo-China, Malesia, and Papuaasia are understudied or even unexplored.

In North America, monographs were published by Clinton (1902, 1904, 1906), Zundel (1939), and Fischer (1953). The smut fungi of Mexico are presented in Durán (1987). Recently, a comprehensive monographic treatment of the smut fungi of Greenland was published by Denchev et al. (2020a). The largest gap of knowledge for this continent is Canada from where only a few articles have been published during the last 50 years.

For Central and South America and the Caribbean, monographs or checklists of smut fungi are published for Costa Rica (Piepenbring 1996), Panama (Piepenbring 2001), Cuba (Piepenbring and Hernández 1998), Colombia (Molina-Valero 1980; Piepenbring 2002a), Bolivia (Piepenbring 2002b), Brazil (Viegas 1944), and the Neotropics (Piepenbring 2003). A monographic treatment of the smut fungi of

Argentina was published by Hirschhorn (1986). Nevertheless, few collection trips focused on this group have been carried out in this part of the world and the smut fungi of Central and South America and the Caribbean continue to be understudied.

In terms of the smut fungi, Africa is the least studied continent. There is a monograph of African smut fungi by Zambettakis (1970, with a supplement in 1980), a monograph of South African smut fungi (Zundel 1938), and checklists of the smut fungi in Africa (Vánky et al. 2011), Ethiopia and Eritrea (Vánky 2005), and Malawi, Zambia, and Zimbabwe (Vánky and Vánky 2002).

For Australasia, there are monographs of the smut fungi of Australia (Vánky and Shivas 2008) and New Zealand (Vánky and McKenzie 2002). Australia is the continent from where the highest number of smut fungi have been described for the last few decades.

Compared to filamentous smuts, the number of discovered yeast taxa in the Ustilaginomycotina is rather small and currently about 50 species are recognized. No yeast-like taxa are known from the Entorrhizomycota. Due to the limited number of observations, geographic distribution patterns of these yeast species are mostly unknown. Often these are also recovered from geographic regions or ecosystems that do not harbour known host species. For example, several asexual species of *Farysia*, which parasitizes hosts belonging to the Cyperaceae, were described from leaves of different plants worldwide with no link to a sexual stage (Inácio et al. 2008; Rush et al. 2020). Often these yeasts are found on the surface of leaves (Fonseca and Inácio 2006; Kemler et al. 2017) and some yeast taxa interact with plants in other ways than do smut fungi. Several new Exobasidiomycetes yeasts (*Entyloma*, *Golubevia*, and *Jamesdicksonia*) for instance were isolated from apples in different countries and were ultimately linked to the postharvest disorder named “white haze”, an intensive fungal growth on the apple fruit surface resulting in a compromised quality of the fruits (Boekhout et al. 2006; Richter et al. 2019). Fungi morphologically similar to the asexual morphs of Ustilaginomycotina were also frequently isolated from air, soils, or animal (including human) samples (reviewed in Boekhout et al. 2011; Begerow et al. 2014, 2018). It is also worth mentioning that some yeast states of smuts (e.g., *Acaromyces*, *Meira*, some members of Microstromatales) are associated with insects or insect frass. Whether these fungi performed a remarkable host-shift or use the insects as vectors requires further studies.

Biased accounts of species diversity to a few regions is a difficulty to estimate the exact number of smut fungi throughout the world. As can be seen from the species descriptions throughout the last decade, it is also clear that a handful of researchers have described the majority of smut fungi in this period. Further problems result from the fact that the species concept in smut fungi have changed from a

purely morphological to a phylogenetic species concept and most species are nowadays described based on molecular markers. This research has shown that smut fungi are highly host specificity, and many species described as multi-host parasites potentially harbor a large number of cryptic species. However, many smut fungal specimens are decades old and it can become difficult to use molecular tools to delimit potential new species. Next to finding unknown species in poorly surveyed regions of the planet, it will also be essential to collect specimens from a majority of already described species throughout the world to understand the real extent of cryptic species diversity.

Describing species diversity of yeast-like taxa faces its own challenges. How to bring about germination and proliferation on artificial media of asexual states of smut fungi has been known for almost 100 years, and isolation of smut-related yeasts is not uncommon. The cultivation of asexual species can be challenging due to their slow growth and special requirements, including low incubation temperatures (Boekhout et al. 2006). Some smuts produce anamorphs in situ, e.g., *Anthracoidea*, *Entyloma*, *Exobasidium*, *Microbotryum*, and *Ustilago*. The characteristics of these asexual morphs unfortunately were rarely studied in detail, however there are exceptions (e.g., Lehtola 1940). As a result, our understanding of growth requirements of asexual states of smuts is mainly based on species described as yeasts. Studies of the physiology of these fungi can potentially improve cultivation success of smuts in the future.

New species publication rate

In the last 11 years 162 new species of smut fungi and related lineages have been described and the numbers of species has risen to over 2000 in 2020. Of the newly described species in the last 11 years, 22 are only known in their asexual yeast stage. It has been suggested that there could be around 4500 species of smut fungi (Vánky 2011a, b). Taking into account the fact that the majority of smut fungi found so far are parasitic on host plants in the Poaceae and Cyperaceae, and the centres of diversity of these plant families are in regions that have not been extensively surveyed for smut fungi, it seems reasonable that the number of species could be double of what is known today.

No estimations of yeast-like taxa phylogenetically related to smuts are available to date, and these fungi show no geographic and host-dependent distribution so far. Therefore, it remains unknown how yeast-like taxa will influence species diversity in Ustilaginomycotina and Microbotryales. Public sequences that are related to smut fungi, but which are not named as independent species, indirectly reflect a larger diversity of yeasts in the two groups. For instance, several genera and possibly families in Exobasidiomycetes await description (Richter et al. 2019). These efforts are hampered

by the ongoing, but yet incomplete, reclassification of teleomorphic smuts and yeast-like forms. Additionally, the formerly polyphyletic yeast genera *Pseudozyma*, *Rhodotorula* and *Tilletiopsis* have been restricted to clades that contain respective type species. Therefore, either taxonomic novelties should be described in already existing sexual genera (e.g., *Entyloma*, *Graphiola*) or in newly erected genera, like in the cases of *Jaminaea*, *Meira*, *Sympodiomycopsis*, and *Violaceomyces* (Table 9; Fig. 14).

Species number in Basidiomycota

The above case studies represent five main groups of basidiomycetes: saprophytes of grass/forest-litter, wood-decaying, ectomycorrhizal, yeast-like and plant parasitic. We calculated the publication rate of new species in each of the groups in the past twelve years (2009–2020; Table 10). Based on the latest taxonomic system of Basidiomycota (He et al. 2019), we applied the publication rate from the case studies to all the same group of Basidiomycota on a family rank. Estimated species number of each order are listed in Table 11. The analysis predicted there will be 54,000 species in Basidiomycota described until 2030.

A total of 41,270 species known in Basidiomycota account for about one third of the known fungal diversity of 144,000 species worldwide (He et al. 2019; Wijayawardene et al. 2020). Thus, we estimate the species number of Basidiomycota to be 1.4–4.2 million worldwide which is the 1/3 of mid-values in previous studies (2.2–3.8 million in Hawksworth and Lücking 2017; 11.7–13.2 million in Wu et al. 2020).

Discussion

Our analyses of species publication rates in the past twelve years and the species numbers in currently recognized families of Basidiomycota predicted more than 54,000 species in Basidiomycota described by 2030. Publication rates of new species differ among taxa and reflect their progress on biodiversity research.

Among the analysed five groups, dimorphic yeast-like basidiomycetes showed the highest new species publication rate (0.0599). A possible explanation is that yeasts are widespread organisms and inhabit a broad range of habitats (Peter et al. 2017). Yeasts grow relatively well on artificial media and their identification is straightforward (Kurtzman et al. 2011; Boekhout et al. 2021). In the past 10 years, numerous taxonomic novelties representing yeast-like fungi (including allied dimorphic taxa) have been discovered from all over the world. Although the majority of publications in that period were dedicated to descriptions of a few species

(usually 1–2 species per publication, Yurkov 2017), more than 100 new species from China were documented in a single study (Li et al. 2020a, b). According to the new species numbers published in the past ten years, the number of known dimorphic yeast-like fungi has rapidly grown, especially in the order *Tremellales*, where several short-term peaks in publication rates were observed (see Fig. 3). It is likely that the same trend will continue and the diversity of dimorphic yeast-like taxa will be increase in the following ten years with more new species and genera described in the future (e.g., Millanes et al. 2021). Exploration of as yet understudied regions and environments, as well as a more precise identification of cryptic morphologically indistinguishable species will substantially contribute to the species diversity in these fungi.

Unlike basidiomyceteous yeasts, the new species publication rate of plant parasitic basidiomycetes was relatively low and rather stable over the time. This is probably because of their obligate parasitic relationship with host plants. The stable number of extant plants restricts the diversity of plant parasitic basidiomycetes to some extent. The fastest rate of new species description in *Puccinia* occurred between 1900 and 1950 (see Fig. 12), and has declined in the last 50 years. The description of new species of plant parasites is biased by their agricultural importance. The smut fungi are well documented in the northern hemisphere, and Europe is well

sampled. In large parts of Asia, Africa and Latin America, where high species diversity must be assumed, only a few studies have been conducted (e.g., Piepenbring et al. 2012).

The rates of publication of sporocarp-forming basidiomycetes differ greatly between taxa. This is probably due to their relatively complex lifestyles and distribution patterns which determine field observations and, thus, the discovery of new species. The species diversity of sporocarp-forming basidiomycetes is insufficiently studied. The highest species diversity is reported from temperate zones (Varga et al. 2019), and it has also been shown to be high in the tropical zone, such as diversity of *Agaricus* (Hyde et al. 2018). Further studies of sporocarp-forming basidiomycetes are needed to understand the diversity of this group of fungi.

The estimated number of 1.4–4.2 million species in Basidiomycota worldwide is much larger than the known diversity. Future discoveries of biodiversity face several challenges from anthropogenic climate change and growing pressure on natural environments, including habitat fragmentation and biodiversity loss. Reliable identification of new species requires a substantial investment of time and resources to document diverse properties such as morphology, physiology, life-cycle, host relationships, and nucleotide sequences not restricted to the common DNA-barcode, ribosomal ITS. High numbers of predicted but yet undescribed species needs the mycological

Table 9 Number of new smut species in different orders published from 2009 to 2020

Sub-Phylum	Class	Order	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	New species publication rate
Ustilaginomycotina	Exobasidiomycetes	Ceraceosorales	-	-	-	-	-	-	-	2	-	-	-	-	0.001 (69/579/12)
		Doassansiales	-	-	-	-	-	-	-	-	-	-	-	-	
		Entylomatales	1	-	-	-	2	4	-	1	3	6	5	-	
		Exobasidiales	5	-	-	4	1	1	-	1	1	1	1	3	
		Georgiefischeriales	-	-	-	-	1	-	-	1	-	-	1	-	
		Golubeviales	-	-	-	-	-	-	-	-	-	-	1	-	
		Microstromatales	-	-	-	-	-	-	-	1	7	1	2	-	
		Robbauerales	-	-	-	-	-	-	-	-	-	-	-	-	
		Tilletiales	3	1	1	-	-	3	-	-	-	4	-	-	
	Malasseziomycetes	Malasseziales	-	-	1	-	-	-	-	3	-	1	-	-	0.0321 (5/13/12)
	Moniliellomycetes	Moniliellales	-	-	-	2	1	-	-	-	-	4	-	-	0.0729 (7/8/12)
	Ustilaginomycetes	Cintractiellales	-	-	-	-	-	-	-	-	-	1	-	1	0.0061 (85/1155/12)
		Uleiellales	-	-	-	-	-	-	-	-	-	-	-	-	
		Urocystidales	1	-	3	2	1	1	1	-	-	2	-	2	
		Ustilaginales	3	-	17	2	15	3	3	3	14	4	2	2	
		Violaceomycetales	-	-	-	-	-	-	2	-	-	-	-	-	
Pucciniomycotina	Microbotryomycetes	Microbotryales	-	-	-	1	1	-	-	-	-	2	1	1	0.0041 (6/122/12)
Based on: Afshan et al. 2020; Aime et al. 2018b; Albu et al. 2015; Bao et al. 2010; Bezerra et al. 2018; Brewer et al. 2014; Cabañes et al. 2011, 2016; Cao et al. 2018; Chamnanpa et al. 2013; Crous et al. 2019; Denchev and Denchev 2011a, 2011b, 2012, 2013, 2016a, 2016b, 2016c, 2018a,b, 2019; Denchev et al. 2010, 2011a, 2011b, 2012, 2013a, 2013b, 2016, 2018, 2019, 2020b; Francesca et al. 2016; Guo and Xu 2013; He et al. 2011; Honnavar et al. 2016; Kennedy et al. 2012; Kijpomyongpan and Aime 2016, 2017; Kruse and Thines 2019; Kruse et al. 2018a, 2018b, 2018c, 2020; Li et al. 2014b, 2017a, 2017b, 2019, 2020; Limtong et al. 2017; Lorch et al. 2018; Lutz et al. 2012; Macedo et al. 2016; McTaggart et al. 2020; Mekha et al. 2014; Nasr et al. 2014, 2017, 2019; Oliveira et al. 2013, 2014; Piątek 2014; Piątek and Shivas 2011; Piątek et al. 2011, 2012a,b, 2013a,b, 2015a,b, 2016; Piepenbring et al. 2012, 2020; Richter et al. 2019; Riess et al. 2019; Rooney-Latham et al. 2017; Rush and Aime 2013; Rush et al. 2020; Savchenko 2015; Savchenko and Carris 2017; Savchenko et al. 2013, 2014a,b, 2016, 2020; Shivas et al. 2011, 2012; Singh et al. 2020; Sipiczky 2020; Stajsic et al. 2018; Sun et al. 2018; Thanh and Hien 2018; Thanh et al. 2012, 2013, 2018; Vánky 2011b, 2013; Vánky and Abbasi 2011a,b; Vánky and Salo 2011; Vánky et al. 2013; Ziegler et al. 2018															

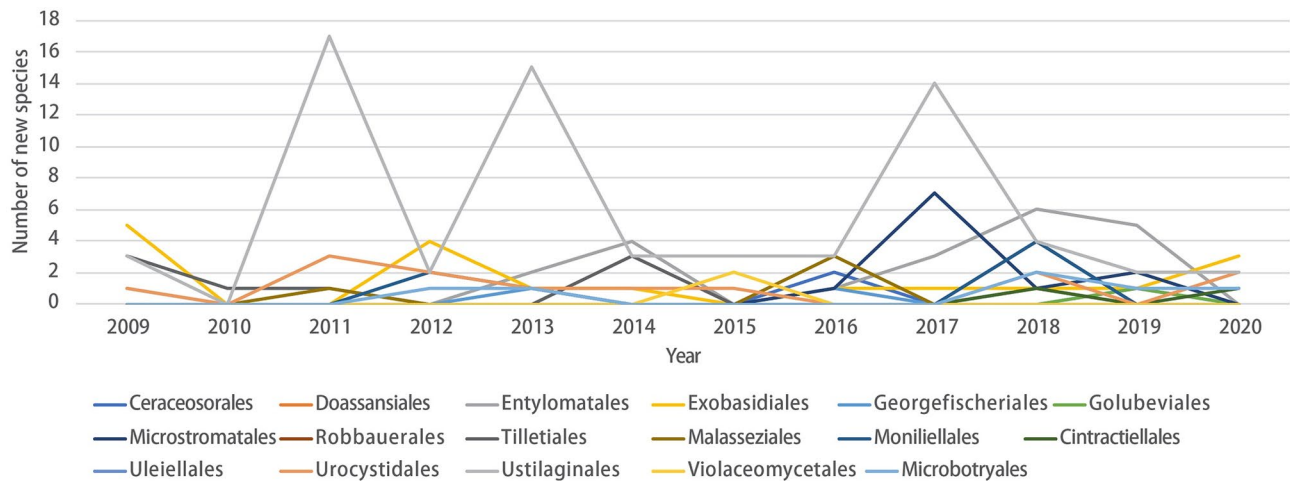


Fig. 14 Line chart of number of new smut species in different orders from 2009 to 2020

Table 10 The estimated species number of case studies

Case study	Groups	Publication rate from 2009 to 2020		Species number in 2020	Estimated species number in 2030
<i>Agaricus</i>	Grass/forest-litter saprobic	0.0412		600	898
<i>Ganoderma</i>	Wood-decaying	0.0313		180	245
Tremellomycetes	Yeast-like	0.0557	0.0599	629	1125
Cystobasidiomycetes		0.2679		59	106
Microbotryomycetes		0.0304		284	508
<i>Gyroporus</i>	Ectomycorrhizal	0.15	0.0465	35	55
<i>Tricholoma</i>		0.0133		250	394
<i>Russula</i>		0.02276		3000	4,726
<i>Cantharellus</i>		0.1154		166	262
Rust*	Plant parasitic	0.0029	0.0199	6798	8275
Exobasidiomycetes		0.001		648	789
Malasseziomycetes		0.0321		18	22
Moniliellomycetes		0.0729		15	18
Microbotryomycetes		0.0041		128	156
Ustilaginomycetes		0.0061		1240	1509

*Rust data including *Aecidium*, *Chrysomyxa*, *Dasyscypha*, *Endoraecium*, *Gymnosporangium*, *Melampsora*, *Milesina*, *Neophysopella*, *Phakopsora*, *Phragmidium*, *Puccinia*, *Pucciniastrum*, *Ravenelia*, *Uredo*, *Uromyces* and *Uromycladium*.

community to speed-up publication rates to formally document diversity in a race against biodiversity loss (Pearce et al. 2020).

In the past decade, molecular tools facilitated the identification of known and novel species of fungi and helped to produce robust single- and multi-gene phylogenies. For

example, large monographic works that introduced large numbers of new species in *Russula* purely based on morphology may presently be viewed doubtful in the modern era of sequence data. Indeed, with the broad introduction of the ITS-barcode (as well as other sequences) to

Table 11 The predicted number of species in each order of the Basidiomycota in 2030

Subphylum	Class	Order	Groups included	Species number estimated in 2030	Total
Agaricomycotina	Agaricomycetes	Agaricales	Wood-decay, grass/forest-litter saprophytic, ectomycorrhizal	24,508	42,700
Agaricomycotina	Agaricomycetes	Amylocorticiales	Wood-decay	50	
Agaricomycotina	Agaricomycetes	Atheliales	Wood-decay	115	
Agaricomycotina	Agaricomycetes	Auriculariales	wood-decay	190	
Agaricomycotina	Agaricomycetes	Boletales	Ectomycorrhizal, wood-decay	3133	
Agaricomycotina	Agaricomycetes	Cantharellales	Ectomycorrhizal Wood-decay	859	
Agaricomycotina	Agaricomycetes	Corticiales	Wood-decay	112	
Agaricomycotina	Agaricomycetes	Geastrales	Grass/forest-litter saprophytic	231	
Agaricomycotina	Agaricomycetes	Gloeophyllales	Wood-decay	52	
Agaricomycotina	Agaricomycetes	Gomphales	Ectomycorrhizal, wood-decay	633	
Agaricomycotina	Agaricomycetes	Hymenochaetales	Wood-decay	1305	
Agaricomycotina	Agaricomycetes	Hysterangiales	Ectomycorrhizal, grass/forest-litter saprophytic	208	
Agaricomycotina	Agaricomycetes	Jaapiales	Wood-decay	2	
Agaricomycotina	Agaricomycetes	Lepidostromatales	Yeast	20	
Agaricomycotina	Agaricomycetes	Phallales	Grass/forest-litter saprophytic	205	
Agaricomycotina	Agaricomycetes	Polyporales	Wood-decay	2772	
Agaricomycotina	Agaricomycetes	Russulales	Ectomycorrhizal, grass/forest-litter saprophytic, Wood-decay	6662	
Agaricomycotina	Agaricomycetes	Sebacinales	Wood-decay	52	
Agaricomycotina	Agaricomycetes	Stereopsidales	–	15	
Agaricomycotina	Agaricomycetes	Thelephorales	Ectomycorrhizal	506	
Agaricomycotina	Agaricomycetes	Trechisporales	Wood-decay	134	
Agaricomycotina	Agaricomycetes	Tremellodendropsidales	–	8	
Agaricomycotina	Dacrymycetes	Dacrymycetales	Wood-decay	149	
Agaricomycotina	Dacrymycetes	Unilacrymales	Wood-decay	1	
Agaricomycotina	Tremellomycetes	Cystofilobasidiales	Yeast	52	
Agaricomycotina	Tremellomycetes	Filobasidiales	Yeast	91	
Agaricomycotina	Tremellomycetes	Holtermanniales	Yeast	23	
Agaricomycotina	Tremellomycetes	Tremellales	Yeast Wood-decay	501	
Agaricomycotina	Tremellomycetes	Trichosporonales	Yeast	109	
Agaricomycotina					
Pucciniomycotina	Agaricostilbomycetes	Agaricostilbales	Yeast	86	
Pucciniomycotina	Atractiellomycetes	Atractiellales	Yeast	104	
Pucciniomycotina	Classiculomycetes	Classiculales	Yeast	7	
Pucciniomycotina	Cryptomycocolacomycetes	Cryptomycocolacales	Yeast	4	
Pucciniomycotina	Cystobasidiomycetes	Buckleyzymales	Yeast	9	
Pucciniomycotina	Cystobasidiomycetes	Cystobasidiales	Yeast	52	
Pucciniomycotina	Cystobasidiomycetes	Erythrobasidiales	Yeast	13	
Pucciniomycotina	Cystobasidiomycetes	Naohideales	–	1	
Pucciniomycotina	Cystobasidiomycetes	Sakaguchiales	Yeast	9	
Pucciniomycotina	Microbotryomycetes	Heterogastridiales	Yeast	4	
Pucciniomycotina	Microbotryomycetes	Kriegeriales	Yeast	13	
Pucciniomycotina	Microbotryomycetes	Leucosporidiales	Yeast	20	
Pucciniomycotina	Microbotryomycetes	Microbotryales	Plant parasitic	156	
Pucciniomycotina	Microbotryomycetes	Sporidiobolales	Yeast	70	

Table 11 (continued)

Subphylum	Class	Order	Groups included	Species number estimated in 2030	Total
Pucciniomycotina	Mixiomycetes	Mixiales	Yeast	2	
Pucciniomycotina	Pucciniomycetes	Helicobasidiales	Plant parasitic	39	
Pucciniomycotina	Pucciniomycetes	Pachnocybales	–	1	
Pucciniomycotina	Pucciniomycetes	Platyglloeales	Plant parasitic, wood-decay	30	
Pucciniomycotina	Pucciniomycetes	Pucciniales	Plant parasitic	7980	
Pucciniomycotina	Pucciniomycetes	Septobasidiales	Plant parasitic	5	
Pucciniomycotina	Spiculogloeomycetes	Spiculogloeales	–	12	
Pucciniomycotina	Tritirachiomycetes	Tritirachiales	Yeast	4	
Pucciniomycotina					8621
Ustilaginomycotina	Exobasidiomycetes	Ceraceosorales	Plant parasitic	4	
Ustilaginomycotina	Exobasidiomycetes	Doassansiales	Plant parasitic	66	
Ustilaginomycotina	Exobasidiomycetes	Entylomatales	Plant parasitic	233	
Ustilaginomycotina	Exobasidiomycetes	Exobasidiales	Plant parasitic	135	
Ustilaginomycotina	Exobasidiomycetes	Georgefischeriales	Plant parasitic	56	
Ustilaginomycotina	Exobasidiomycetes	Golubeviales	Yeast	4	
Ustilaginomycotina	Exobasidiomycetes	Microstromatales	Plant parasitic	58	
Ustilaginomycotina	Exobasidiomycetes	Robbauerales	Yeast	2	
Ustilaginomycotina	Exobasidiomycetes	Tilletiales	Plant parasitic	233	
Ustilaginomycotina	Malasseziomycetes	Malasseziales	Yeast	38	
Ustilaginomycotina	Moniliellomycetes	Moniliellales	Yeast	20	
Ustilaginomycotina	Ustilaginomycetes	Urocystidales	Plant parasitic	355	
Ustilaginomycotina	Ustilaginomycetes	Ustilaginales	Plant parasitic	313	
Ustilaginomycotina	Ustilaginomycetes	Cintractiellales	Plant parasitic	1	
Ustilaginomycotina	Ustilaginomycetes	Ustilaginales	Plant parasitic	837	
Ustilaginomycotina	Ustilaginomycetes	Uleiellales	Plant parasitic	2	
Ustilaginomycotina	Ustilaginomycetes	Violaceomycetales	Yeast	2	
Ustilaginomycotina					2359
Wallemiomycotina	Wallemiomycetes	Geminibasidiales	Grass/forest-litter saprophytic	3	
Wallemiomycotina	Wallemiomycetes	Wallemiales	Grass/forest-litter saprophytic	12	
Wallemiomycotina					15
Total					53,695

“–” means group uncertain

characterize species, the weight in species recognition is frequently given not to morphological characters but to the interpretation of nucleotide differences, especially since most new species are now often described by young mycologists with little experience with morphological recognition. This situation illuminates a lack of mycologists with broad taxonomic skills and highlights the necessity to educate more young mycologists in rapidly developing regions, like Asia (Hyde et al. 2020a, b).

To efficiently explore the species diversity in Basidiomycota, both temporally and geographically, a joint global initiative by mycologists is needed. In the past ten years, diversity, ecology and systematics of basidiomycetes were studied globally, though the particular focus of the studies

differed among the taxa. In sporocarp-forming fungi, *Agaricus* was intensively studied in an international collaboration between Asian, European and USA researchers. As a result, a large number of new species were described from in the tropical zones of China and Thailand, making that area the primary source of new species in the last decade. A robust system for classification of *Agaricus* species was established and a total of 178 *Agaricus* species were described worldwide (Zhao et al. 2011, 2016a, b; Chen et al. 2017; He et al. 2017; Callac and Chen 2018). Thus, we appeal for a broad global collaboration focusing on biodiversity and taxonomic studies in Basidiomycota in the future, not only in well-explored areas, but also other unexplored regions.

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