

# Molecular techniques revolutionize knowledge of basidiomycete evolution

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**Abstract** A brief survey towards an understanding of evolution of *Basidiomycota* in the last five decades is given. Between 1960–1990 studies were based mainly on morphology, subcellular structure, biochemistry, physiology and ecology. In the last 20 years, molecular methods have revolutionized the study of taxonomy, systematics, phylogeny, biogeography, population and microevolutionary processes in basidiomycetes. A fundamental improvement in the understanding of evolution of basidiomycetes has been achieved. It is anticipated that numerous new taxa at different taxonomic levels will be recognized based on integrated approaches, and new data will soon provide fascinating insights into the origin, evolution and biogeography of basidiomycetes in the coming years.

**Keywords** Biogeography · Fungi · Phylogeny · Taxonomy · Systematics

## Introduction

The phylum *Basidiomycota* is typically characterized by the presence of a basidium bearing sexual spores (i.e., basidiospores) in addition to several other characters (Oberwinkler 1978). A common informal term for all *Basidiomycota* is “basidiomycetes”. This is a very important group, being the second largest assemblage of the Kingdom *Fungi*, comprising approximately 31,000 described species (Kirk et al. 2008). The group is of almost

cosmopolitan in distribution, encompassing numerous edible mushrooms, toadstools, pathogens, and endophytes besides numerous mycorrhizal partners and wood-rotting decomposers in forest ecosystems. The basidiomycetes have, as a result, drawn the attention of mycologists for a long time, since the very beginning of scientific mycology at the 18th century (e.g. Persoon 1801; Fries 1821; de Bary 1853, 1866; Brefeld 1888). Knowledge of the taxonomy, host range and distribution, phylogeny and evolution of this group of fungi has rapidly increased in the last 50 years. This is especially evident in the last 20 years with the development of molecular techniques.

The aim of paper is to summarize the last 50 years of research in the *Basidiomycota*, and also to review our present understanding of the phylum, emphasizing the highlights among selected groups and future perspectives. No attempt has been made to cite all of the relevant studies for the *Basidiomycota*, because studies on individual groups of basidiomycetes are too numerous to list.

## The earlier thirty years: taxonomic and systematic researches

Between 1960–1990 gross phenotypic taxonomy was supplemented by microscopy and in vitro culturing (e.g. Miller 1971; Desjardin 1990). Many groups of basidiomycetes were intensively studied. At the same time important monographic or taxonomic works were published. A few of the most influential ones may be mentioned here; they are Corner (1966), Horak (1968), Cummins and Hiratsuka (1983), Pegler (1983), Vánky (1987), although there are many others.

In Europe, compilation and publication of a few important regional mycota, such as British Fungus Flora (1979–), and Flora Agaricina Neerlandica (1988–), have successfully been

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launched and promoted, with welcomed works by Moser (1983), Hjortstam et al. (1987, 1988), and Ryvarden and Gilbertson (1993, 1994). The monographic works “Fungi Europaei” (1984–) have been valuable references in the study on diversity of macromycetes both within and outside Europe. During the same period in North America, mycologists also were very active in studying basidiomycete diversity (e.g. Hesler and Smith 1979; Petersen 1981; Halling 1983; Mueller 1992). In East Asia, the mycota of Japan has been studied much more intensively than in any of the other countries in the region (e.g. Imazeki et al. 1988; Hiratsuka et al. 1992). The Flora Fungorum Sinicorum (1987–), covers such a diverse group of fungi that they can be finished only when specific groups have been intensively studied, and thus the publication will probably take several decades, although over 10 volumes on basidiomycetes in China are now available (e.g. Peng et al. 1992; Zhuang et al. 1998; Guo 2000; Yang 2005a; Zang 2006; Zhou 2007). Basidiomycetes in the Southern Hemisphere have also received much attention from a number of fungal taxonomists (e.g. Cunningham 1965; Dennis 1970; Heinemann 1972; Reid 1980; Garrido 1988).

With regard to the systematics and phylogeny of basidiomycetes, the works of Singer (1962, 1986), Donk (1964, 1971), Gäumann (1964), Kreisel (1969), Ainsworth et al. (1973), Oberwinkler (1977, 1978, 1982, 1985), Kühner (1980) and Jülich (1981) are probably among the most influential between 1960 and 1990. The gasteromycetes were often treated a single group, although some, such as the secotioid taxa, have anatomical similarities to certain agarics and boletes, and, as a result, were supposed to be related to agarics and boletes respectively. However, views were in conflict as regards to the direction of the evolutionary process (Singer and Smith 1960; Heim 1971; Thiers 1984; Singer 1986). Oberwinkler (1977, 1978), Thiers (1984) and others argued that it was more likely that sequestrate (secotioid or gasteroid) basidiomycetes were derived repeatedly and convergently, and should not be regarded as a single natural group.

In trying to elucidate the phylogeny of basidiomycetes, Oberwinkler (1982) exquisitely discussed the significance of the morphology of the basidium, together with the knowledge of the presence or absence of secondary spores, the host specificity and other aspects, and he pointed out that the evolution of the homobasidiomycetes from a phragmo- and/or holobasidial ancestral form was probably accompanied by the loss of the capacity to form secondary spores, and the formation of uniform basidium. Due to the unique basidial morphology, the connections of several groups of gasteromycetes with other basidiomycetes were unknown (Oberwinkler 1982).

Besides the morphology of basidia, spindle pole bodies (e.g. McLaughlin et al. 1995; Celio et al. 2006), and septa

(e.g. Moore 1985, 1997; Khan and Kimbrough 1982; Oberwinkler and Bandoni 1982; Kimbrough 1994; Wells 1994; McLaughlin et al. 1995; Bauer et al. 1997; Müller et al. 2000; Hibbett and Thorn 2001; Van Driel et al. 2009) as well as physiological and biochemical characteristics (Bartnicki-Garcia 1968; Van der Walt and Yarrow 1984; Prillinger et al. 1993; Kurtzman and Fell 1998; Boekhout and Guého 2002) have significantly contributed to the systematics of basidiomycetes until the present day. The structural and biochemical database for fungi (Celio et al. 2006) aims to capture several of these characters in a comprehensive manner.

At the same time, for some groups of basidiomycetes that grow in culture, mating studies have been used to elucidate the specific or supraspecific consistency (Korhonen 1978a, b; Gordon and Petersen 1991; Petersen and Halling 1993; Petersen and Gordon 1994).

### 1990–2010: a transition from morphologically-based taxonomy and systematics to molecular-based phylogeny and evolution

Morphological and physiological studies left many questions and controversies unresolved, due in part to the paucity of characters, as well as the general absence of explicit phylogenetic analyses (Hibbett 2007). During the last 20 years, remarkable progress has made in the study of molecular evolution of basidiomycetes with the introduction of molecular methods.

The development of new statistical methods and advances in computational technology make the evaluation of evolution possible. In particular, with the invention and the development of the polymerase chain reaction (PCR) technique, phylogenetic analysis of DNA or protein sequences has become a powerful tool for studying molecular evolution in fungi (White et al. 1990; Bruns et al. 1992; Nei and Kumar 2000). Ribosomal DNA (rDNA) sequences have provided a wealth of information concerning phylogenetic relationships (Hillis and Dixon 1991), and studies of rDNA sequences have been used to infer phylogenetic history across a very broad spectrum, from studies among the basal lineages of life to relationships among closely related species and populations. Sequence data from ribosomal DNA (i.e. nSSU and nLSU rDNA), mtDNA and protein coding genes (e.g. *tef1*, *rpb1*, *rpb2*) have been used in fungal systematic studies (e.g. Swann and Taylor 1995; Fell et al. 2000; Lutzoni et al. 2004; Matheny et al. 2007a, b, c).

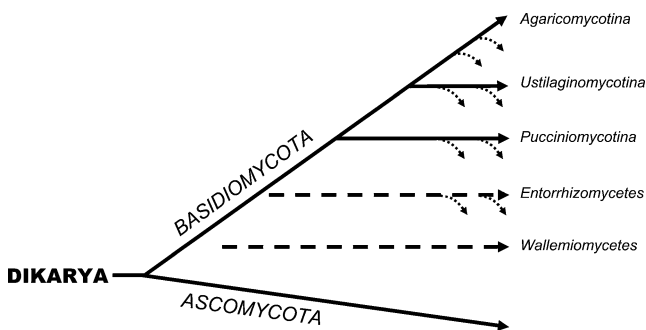
#### Classification in the basidiomycota

Before the molecular era, basidiomycetes were usually divided into Phragmobasidiomycetes and Holobasidiomy-

etes, or Heterobasidiomycetes and Homobasidiomycetes. Molecular phylogenetic data showed that a separation of heterobasidiomycetes from homobasidiomycetes is impossible, and, thus, such historical concepts have to be abandoned (Weiß et al. 2004a).

Molecular phylogenetic studies have led to significant advances in the understanding of the higher-level relationships of basidiomycetes, and consequently, the whole taxonomic hierarchy of the *Basidiomycota*, as in the remaining other groups of the *Fungi*, has been dramatically altered. Under the umbrella of the Deep Hypha Research Coordination Network and Assembling the Fungal Tree of Life project (Lutzoni et al. 2004; Blackwell et al. 2007), and additional projects, a few major publications elucidating relationships within the *Fungi* appeared in the last few years (Bauer et al. 2006; James et al. 2006; Liu et al. 2006; Aime et al. 2007). Within the Kingdom *Fungi*, molecular phylogenetic analyses support the monophyly of the *Ascomycota* and *Basidiomycota*, and these are regarded as the subkingdom *Dikarya* (James et al. 2006). A comprehensive classification of *Fungi* based on phylogenetic results was proposed (Hibbett et al. 2007) and adopted by the Dictionary of the *Fungi* (Kirk et al. 2008).

Recognized as a phylum, the phylogeny of *Basidiomycota* has been extensively revisited and many new taxa including diverse taxonomic ranks below the phylum level have been proposed in the last few years based on molecular phylogeny and reevaluation of morphological characters. The phylum *Basidiomycota* is generally regarded as having three major clades (Fig. 1; Swann and Taylor 1995; Lutzoni et al. 2004; Taylor et al. 2004; Bauer et al. 2006; Matheny et al. 2007a, b), the *Pucciniomycotina* (Urediniomycetes, Fig. 2a–d), the *Ustilaginomycotina* (Ustilaginomycetes, Fig. 2f–h), and the *Agaricomycotina* (Hymenomycetes, Fig. 2i–t), with the phylogenetic positions of additional two major lineages, the *Entorrhizomy-*



**Fig. 1** A simplified schema of the classification of the phylum *Basidiomycota*, mainly based on Hibbett et al. (2007) and Matheny et al. (2007b, c). Dashed-line arrows indicate taxa that are of uncertain placement; dotted-line arrows indicate ancient and recent gasteromycetations

*etes* (Fig. 2e) and *Wallemiomycetes* yet unclear (Table 1; Zalar et al. 2005; Matheny et al. 2007c; Hibbett et al. 2007).

It is worthy and interesting to note that Moncalvo et al. (2002) highlighted the complexity of the history of the *Agaricomycotina*. They found that many clades correspond to traditional taxonomic groups, many do not, and several clades are best supported by ecological, biochemical, or trophic habits rather than by morphological similarities. Such or similar phenomena may be revealed in many other groups of *Fungi*.

#### Gasteromycetation

Within the *Basidiomycota*, “gasteromycetes” (with spores that are not forcibly discharged, statismospores, see Figs. 1 and 3e, rather than forcibly discharged, ballistospores, see Fig. 3b) comprise a diverse, artificial assemblage of puffballs, earthstars, false earthstars, earthballs, bird’s nest and cannonball fungi, stinkhorns, secotioid agarics and boletes, and false truffles (Reijnders 1963; Heim 1971; Miller and Miller 1988). Molecular systematics studies have revealed that gasteromycetes have independently evolved many times within the basidiomycetes during the adaptation of environmental selective pressures, such as arid conditions, dispersal vectors, and unknown mechanisms (Fig. 1; Bruns et al. 1989; Hibbett et al. 1997; Peintner et al. 2001; Binder and Bresinsky 2002; Binder et al. 2006; Henkel et al. 2010), as were suggested by Oberwinkler (1977, 1978, 1985), Thiers (1984) and many others. It was suggested that the evolution of the sequestrate state to be irreversible (Hibbett 2004, 2007).

The groups of the gasteromycetes whose connections with other basidiomycetes were unknown (Oberwinkler 1982) were revealed as either clades represented entirely by sequestrate taxa, i.e. *Gaeastrales* (Fig. 2n), *Hysterangiales* (Fig. 2q) and *Phallales* (Fig. 2p), or consisting of both sequestrate and non-sequestrate taxa, such as, *Gomphales* (Fig. 2o). The remaining groups, such as “*Lycoperdales*”, “*Nidulariales*”, and “*Tulostomatales*” have close relationships with *Agaricaceae* s.l. (Fig. 2r, s), while “*Melanogastreales*” and “*Sclerodermatales*” show phylogenetic affinity with *Boletales* (Hibbett et al. 1997; Vellinga 2004; Binder and Hibbett 2007; Hosaka et al. 2007; Fig. 2t).

Interestingly, some sequestrate fungi represent recent, divergent events that led to one or a few sequestrate species within a clade of non-sequestrate relatives (Fig. 3; e.g. Kretzer and Bruns 1997; Martin et al. 1999; Vellinga et al. 2003; Vellinga 2004; Albee-Scott 2007; Lebel and Catcheside 2009; Justo et al. 2010), while others of earlier origin have speciated and radiated across a wide spectrum of taxa (Fig. 1; e.g. Binder and Hibbett 2007; Hosaka et al. 2007). Newly most optimal models suggest that the net diversifica-



**Fig. 2** Diverse forms of spore-producing structures in *Basidiomycota*. **a–d.** Species of *Pucciniomycotina*. **a.** *Puccinia recondita* (*Pucciniales*, aecial stage) on *Thalictrum rutifolium*. **b.** *Chrysomyxa succinea* (*Pucciniales*, telial stage) on *Rhododendron* sp. **c.** *Jola* cf. *javensis* (*Platyglloeales*) on moss. **d.** *Sphacelotheca* sp. (*Microbotryales*) on *Polygonum* sp. **e.** *Entorrhiza casparyana* (*Entorrhizomycetes*) on *Juncus articulatus*. **f–h.** Species of *Ustilaginomycotina*. **f.** *Ustilago nuda* (*Ustilaginales*) on *Hordeum vulgare* var. *nudum*. **g.** *Anthracoidea filamentosae* (*Ustilaginales*) on *Carex crebra*. **h.** *Exobasidium deqi-*

*nense* (*Exobasidiales*) on *Rhododendron* sp. **i–t.** Species of *Agaricomycotina*. **i.** *Dacrymyces yunnanensis* (*Dacrymycetales*) on rotten wood. **j.** *Auricularia auricula* (*Auriculariales*) on rotten wood. **k.** *Tremellodendropsis tuberosa* (*Auriculariales*). **l.** *Sebacina incrustans* (*Sebacinales*). **m.** *Multiclavula sinensis* (*Cantharellales*, basidiolichen). **n.** *Geastrum sacatum* (*Geastrales*). **o.** *Ramaria hemirubella* (*Gomphales*). **p.** *Phallus luteus* (*Phallales*). **q.** *Phallo-gaster saccatus* (*Hysterangiales*). **r.** *Agaricus bisporus* (*Agaricales*). **s.** *Crucibulum laeve* (*Agaricales*). **t.** *Boletus reticuloceps* (*Boletales*)

**Table 1** Summary of recent phylogenetic classification of the basidiomycetes

The statistics of the number of the taxa were based on Hibbett et al. (2007) and Kirk et al. (2008), and published data since 2007 which were not included in Kirk et al. (2008). Numbers of species of the three subphyla were rounded to the whole hundreds

Phyllum <i>Basidiomycota</i>				
subphylum			position unknown	
<i>Pucciniomycotina</i>	<i>Ustilaginomycotina</i>	<i>Agaricomycotina</i>	<i>Entorrhizomycetes</i>	<i>Wallemiomycetes</i>
8 classes	2 classes	3 classes	1 class	1 class
18 orders	9 orders	23 orders	1 order	1 order
34 families	28 families	119 families	1 families	1 families
242 genera	117 genera	1146 genera	2 genera	1 genus
8300 species	1700 species	21000 species	15 species	3 species

tion rate of gasteroid forms exceeds that of non-gasteroid forms, and that gasteroid forms will eventually come to predominate over non-gasteroid forms in the clades in which they have arisen (Wilson et al. 2011).

### Species criteria: challenge and opportunity

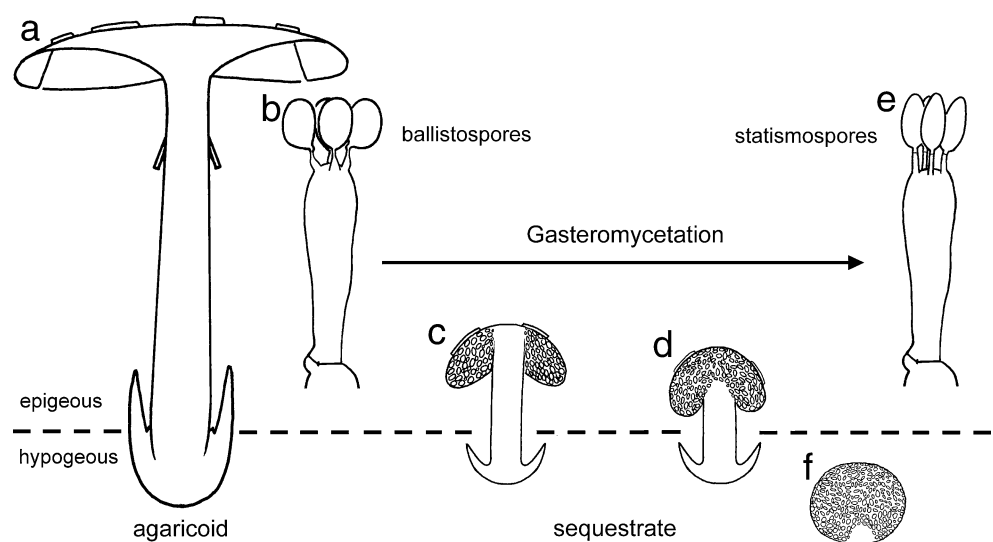
The basic rank in taxonomy of organisms is the species. Attempts to reach a consensus for a universal definition of species have been unsuccessful, and consequently over 20 different concepts have been used (Mayden 1997). For instance, the morphological species concept, the biological species concept, the ecological species concept, and the phylogenetic species concept virtually emphasize morphological divergence, reproductive isolation, adaptation to a particular ecological niche, and nucleotide divergence respectively (Giraud et al. 2008). However, these species criteria correspond to the different events that occur during lineage separation and divergence, rather than to fundamental differences of what is considered to represent a species (de Queiroz 1998, 2007; Giraud et al. 2008).

Morphological species concept is the classic approach used. However, exactly what different mycologists consider to be a species can vary widely, and there are different

approaches for delineating them. In addition, many morphological characters are plastic or subtle, and difficult to assess. It has been repeatedly shown that similar characters can arise from evolutionary convergence or environmental constrains (Moncalvo 2005; Hibbett 2007), and, thus, morphological species concept is, in many cases, unsatisfactory for applications. The application of biological species concept or ecological species concept to fungi was favored between 1960–1990, and is still presently being used. However, there are still many limitations for its application (Taylor et al. 2000; Giraud et al. 2008).

Phylogenetic approaches and incorporation of molecular biological techniques, particularly the analysis of DNA nucleotide sequences have provided new information and the phylogenetic species concept is becoming a popular trend, particularly, when it is applied to asexual organisms, and connects the anamorph and teleomorphic stages of a single species (Guarro et al. 1999; Moncalvo 2005; Hyde et al. 2011). In fungi, the sequence data from the internal transcribed spacer region of the nuclear rDNA locus (ITS) have often been used to recognize fungal phylogenetic species and may well be the DNA barcoding locus used in barcoding (Seifert 2009; Begerow et al. 2010; Jargeat et al. 2010). However, it is better to use multigene genealogy

**Fig. 3** A schema of gasteromycetation in *Amanita* (*Agaricales*). *Torrendia* (Fig. 3c, d) and *Amarrendia* (Fig. 3f) were regarded as genera independent from *Amanita* (Fig. 3a) by several authors (e.g. Bas 1975; Miller and Horak 1992; Bougher 1999; Bougher and Lebel 2002). Recent molecular phylogenetic analyses showed that species of these two genera just present gasteromycetations within *Amanita* (Justo et al. 2010)



concordance than to use a single gene to recognize species (Taylor et al. 2000). The current “gold standard” genealogical concordance phylogenetic species recognition criterion has proved very useful in fungi, because it is more finely discriminating than the other criteria in many cases. Genealogical concordance phylogenetic species recognition has been practiced recently in different groups of basidiomycetes (e.g. Kauserud et al. 2006; Jargeat et al. 2010; Van de Putte et al. 2010).

## Prospects

Fungi play critically important roles in ecosystems, and their potential economic benefits as food and medicine are great. The importance of basidiomycetes in ecosystems as mycorrhizal partners, plant pathogens and decomposers cannot be overestimated. Although understanding of the origin and evolution of basidiomycetes has greatly been improved in recent years and has provided interesting new insights into the phylogeny and natural classification of *Fungi*, it is still far from satisfactory, as many issues relating to their taxonomy and phylogeny, ecology, and geographical distributions remain unclear. In the near future, the following aspects should be a few focal points of research interests:

### 1) Accelerating the discovery and documentation of new taxa

It is generally accepted that only 5–10% of species on the earth have been discovered and named. An estimated 1.5 million fungal species exist and at most only about 5% of the fungal species on the Earth have been discovered (Hawksworth 1991, 2001). Major of the taxa of *Fungi* need to be uncovered (e.g. Jones et al. 2011). A recent estimation of worldwide diversity of macrofungi, including basidiomycetes and ascomycetes with large, easily observed spore-bearing structures that form above or below ground, calculated only 16–41% of macrofungi to be known to science and that endemism levels for macrofungi may be as high as 40–72% (Mueller et al. 2007). Bauer et al. (2006) pointed out that the ca. 8,000 described species of the simple-septate basidiomycetes may only represent the tip of the iceberg of this tremendous morphological and ecological diversified group.

On the other hand, it was assumed that *Fungi* are widely distributed, and consequently, for instance, many European or North American names were applied to morphologically similar Asian fungi. Recent data has shown that some species of *Fungi*, either saprotrophic or ectomycorrhizal or pathogenic, are indeed intercontinentally widely distributed, while many others are restricted in their range (Dai et al. 2003; Li et al. 2009; Liang et al. 2009; Dai 2010; Desprez-Loustau et al. 2011; O'Donnell et al. 2011). In consideration of global changes and dramatic deterioration of environments, largely due to human activities, acceleration

of the inventory of fungi including basidiomycetes is an urgent task (Mueller et al. 2004; Piepenbring 2007).

Over the course of evolution, innumerable fungal taxa, such as plants and animals, have become extinct. Some unknown “living fossils” or unique taxa of basidiomycetes may be found in associated with plant living fossils. For instance, *Bartheletia paradoxa*, growing on leaf litter of *Ginkgo biloba* has a unique septal structure, and, like *G. biloba*, is a living fossil at the basal branching of the *Agaricomycotina*, which apparently used *G. biloba* as its Noah's Ark (Scheuer et al. 2008). Taxa of significance in elucidating the phylogeny of *Basidiomycota* could well be harbored on living fossils of plants (e.g. Manchester et al. 2009). On the other hand, numerous previously unknown or little-known taxa in the tropics (Oberwinkler and Bauer 1990; Isaac et al. 1993; Watling et al. 2002) and on diverse substrates in other regions will contribute to a better understanding of the fungal diversity and evolution (e.g. Piepenbring 1996, 2007; Kirschner et al. 2001a, b; Kirschner and Chen 2004; Binder et al. 2006; Choeyklin et al. 2009; Coelho et al. 2009; Kirschner et al. 2010; Weiß et al. 2004b, 2011).

Molecular-data-based fungal systematics and phylogenetics have evolved very rapidly in the last two decades. However, morphological characters and ultrastructure, ecological traits, biochemical characters, chemical secondary metabolites as well as molecular phylogeny are all equally important in the understanding the evolution of the basidiomycetes. For instance, many hypotheses proposed in the last century based on morphology, ultrastructure, structure of pigments or metabolites have been verified by molecular approaches in the last two decades. To understand the megadiversity of basidiomycetes, multiple methodologies, thus, should be used (Bauer et al. 2001; Petersen and Hughes 2007; Wannathes et al. 2009; Hyde et al. 2010), although the shift from classical to molecular fungal taxonomy and systematics is becoming popular and inevitable (Seifert 2009). It may be worthy to mention that the integration of the on-going efforts of DNA barcoding into the inventory will accelerate the recovery and precise identification of a large number of unculturable, microscopic, and cryptic taxa of basidiomycetes (Moncalvo 2005; Begerow et al. 2010; Jargeat et al. 2010).

It is anticipated that numerous species, some monophyletic groups representing generic and suprageneric new taxa should be recognized within the *Basidiomycota* in the next few years (e.g. Binder et al. 2010). However, taxonomy, including fungal taxonomy, faces serious challenges (Agnarsson and Kuntner 2007), and thus, fungal taxonomists should consider adopting new modes of working (Hibbett et al. 2011), in order to accelerate the discovery and documentation of the world's fungal heritage.

### 2) Genome-based analyses of phylogeny and functional evolution

There has been a dramatic growth in multilocus fungal phylogenies in the last few years. Analyses of multigene sequences have resolved many major clades of *Fungi*, and have enabled development of a higher-level classification for the kingdom (e.g. Hibbett et al. 2007). Nevertheless, the framework is complete, but detailed information within the framework is largely absent, and there are some problematic deep nodes that are not well resolved, which limits our understanding of the evolutionary history of the *Fungi* (McLaughlin et al. 2009). Complete fungal genomes may reveal robust deep nodes of fungal tree of life (Fitzpatrick et al. 2006; Kuramae et al. 2006).

The use of high-throughput sequencing or next-generation sequencing technologies can produce dozens of gigabases per day. Future studies based on genomic data coupling efficient informatics approaches (e.g. Liu et al. 2009; Löytynoja and Goldman 2009) may contribute to the resolution of the major problematical nodes in the phylogeny of basidiomycetes and provide insight into its morphological, ecological and functional evolution. For instance, genome-based analyses may well resolve the backbone of the *Agaricomycotina* phylogeny and elucidate the diversity and evolution of the white rot and brown rot wood-decaying modes and shifts among hosts.

### 3) Biogeographic inference

In comparison to plant or animal biogeography, biogeography of fungi is at its very young stages. For instance, understanding of the role of long distance dispersal of spores in the maintenance of fungal species cohesion is in its infancy. Some data suggest that fungal spores are seldom dispersed for distances greater than 100 m indicating that despite rare long distance dispersal events, significant gene flow via spore dispersal even between islands within Hawaii is quite unlikely (Bergemann and Miller 2002; Burnett 2003), while others suggests that a single fungal species can sustain appreciable gene flow across virtually global distributions (James et al. 2001; Petersen and Hughes 2007).

Biogeographic studies in fungi were impeded by the poor knowledge concerning the accurate distribution of fungal species. Up to now, biogeography of diverse groups of basidiomycetes is still very speculative and is only supported by fragmentary observations. Studies based only on morphological characters may provide a very incomplete and oversimplified picture of distribution patterns and associated historical events (Wu et al. 2000). Many intriguing morphological similarity based geographic distribution patterns, such as the well-known “Asa Gray disjunction” or a vicariance pattern in the Grayan distribution, and the Gondwanan distribution observed in the past (e.g. Horak 1983; Redhead 1989; Halling 2001; Mueller et al. 2001; Yang 2005b; Petersen and Hughes 2007), could well be inferred by molecular phylogenetic analyses in

order to provide a much better understanding of their origin, historical biogeography and dispersal.

A more detailed and accurate understanding of the origin and evolution of a few selected groups of basidiomycetes have been revealed in the last few years, and are compelling areas for future research. For instance, through analyses of ITS and 26S rDNA sequences, and mt-ssu rDNA, Hibbett (2001) demonstrated that there are two main clades of the genus *Lentinus*, one in the New World, the other in the Old World. The Old World/New World disjunction could be due to fragmentation of an ancient Laurasian range. An alternative Gondwanan hypothesis is not supported by the molecular clock age estimates. Only one long distance dispersal event must be invoked in *Lentinula*, that being between Australia and New Zealand. Despite having airborne spores, long distance dispersal is rare in *Lentinula*. Aanen et al. (2002) showed that the symbiosis between fungus-growing termites and their fungal symbionts, *Termitomyces*, has a single African origin and that secondary domestication of other fungi or reversal of mutualistic fungi to a freeliving state has not occurred, and host switching has been frequent, especially at the lower taxonomic levels, and nests of single termite species can have different symbionts.

Recently, Hosaka et al. (2008) elucidated the biogeography of false truffles in the *Hysterangiales*. Their data are consistent with an Australian, or eastern Gondwanan origin of these fungi with subsequent range extensions into the Northern Hemisphere. A mosaic of vicariance and long distance events appears most plausible to explain the current distribution patterns in the false truffles. Using a relaxed molecular clock method, Matheny et al. (2009) reconstructed a phylogeny of the *Inocybaceae* with a geological timeline. Their data showed that the *Inocybaceae* initially diversified no later than the Cretaceous in Palaeotropical settings, in association with angiosperms. Diversification within major clades of the family accelerated during the Palaeogene in north and south temperate regions, whereas several relictual lineages persisted in the tropics. Both vicariance and dispersal patterns are detected. Species from Neotropical and south temperate regions are largely derived from immigrant ancestors from north temperate or Palaeotropical regions.

Without any doubt, more and more such studies on historical biogeography and evolution of different groups of basidiomycetes will soon appear.

### 4) Study on species complex and cryptic species: to understand speciation and adaptation

Fungal speciation is one of the most fundamental issues of mycology (Kohn 2005; Giraud et al. 2008). The advent of molecular biology in the last 20 years has dramatically improved our ability to reveal cryptic diversity, speciation, and local adaptation in basidiomycetes. Recent studies have shown that many morphospecies are complex or aggregates

of taxa with distinct geographic, ecological or pathological traits, comprising several biological and/or phylogenetic species (e.g. Le Gac et al. 2007; Geml et al. 2008; Stubbe et al. 2010; O'Donnell et al. 2011).

It was found that there is often strong host specialization in basidiomycetes (e.g. Piepenbring et al. 1999; Begerow et al. 2004; Shefferson et al. 2007). However, high host specificity does not exclude possibilities for host shifts/host jumps, i.e., evolutionary lability (Parker and Gilbert 2004). Indeed, host jumps and host shifts are thought to be major driving forces in the evolution of basidiomycetes (Roy 2001; den Bakker et al. 2004; Refrégier et al. 2008; Li et al. 2009; Vercken et al. 2010; Li et al. 2011; Rochet et al. 2011). The next generation of high-throughput DNA sequencing methodologies, taking into account not only multilocus markers but also genome-wide studies, will provide enormous amounts of data for the study of phylogeny and population genetics, the reconstruction of patterns of origin and speciation in both time and space of basidiomycetes, leading to a more complete understanding of evolutionary and adaptation processes. The availability of molecular tools will prompt and yield a large number of new and highly interesting results in the near future.

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