

The good, the bad and the tasty: The many roles of mushrooms

K.M.J. de Mattos-Shipley^{1,2}, K.L. Ford¹, F. Alberti^{1,3}, A.M. Banks^{1,4}, A.M. Bailey¹, and G.D. Foster^{1*}

¹School of Biological Sciences, Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK; ²School of Chemistry, University of Bristol, Cantock's Close, Bristol, BS8 1TS, UK; ³School of Life Sciences and Department of Chemistry, University of Warwick, Gibbet Hill Road, Coventry, CV4 7AL, UK; ⁴School of Biology, Devonshire Building, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK

*Correspondence: G.D. Foster, Gary.Foster@bristol.ac.uk

Abstract: Fungi are often inconspicuous in nature and this means it is all too easy to overlook their importance. Often referred to as the “Forgotten Kingdom”, fungi are key components of life on this planet. The phylum *Basidiomycota*, considered to contain the most complex and evolutionarily advanced members of this Kingdom, includes some of the most iconic fungal species such as the gilled mushrooms, puffballs and bracket fungi. Basidiomycetes inhabit a wide range of ecological niches, carrying out vital ecosystem roles, particularly in carbon cycling and as symbiotic partners with a range of other organisms. Specifically in the context of human use, the basidiomycetes are a highly valuable food source and are increasingly medicinally important. In this review, seven main categories, or ‘roles’, for basidiomycetes have been suggested by the authors: as model species, edible species, toxic species, medicinal basidiomycetes, symbionts, decomposers and pathogens, and two species have been chosen as representatives of each category. Although this is in no way an exhaustive discussion of the importance of basidiomycetes, this review aims to give a broad overview of the importance of these organisms, exploring the various ways they can be exploited to the benefit of human society.

Key words: Agaricomycete, Basidiomycete, Model species, Mushroom.

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INTRODUCTION

The basidiomycetes are a large and incredibly diverse phylum of fungi, which, together with the ascomycetes, make up the sub-kingdom *Dikarya* – often referred to as the “higher fungi”. Basidiomycetes are almost exclusively filamentous fungi that have complex lifecycles, reproduce sexually and produce basidiospores on specialised cells called basidia. This review has chosen to focus specifically on the class *Agaricomycetes*, which make up 98 % of the *Agaricomycotina* – the largest subphylum of the basidiomycetes. Taxonomically, *Agaricomycetes* is roughly analogous to the previously accepted *Homobasidiomycetes*, a name which is no longer used due to the recognition that not all members of this phylogenetic group have homobasidia (undivided basidia). *Agaricomycetes* includes the most conspicuous basidiomycete species, all of which produce basidiocarps, such as the gilled mushrooms, bracket fungi, puffballs, crust fungi, chanterelles, coral fungi and jelly fungi (Hibbett 2006).

The morphology of agaricomycete fungi is incredibly varied. The cyphelloid fungi, for example, produce small cup or tube-shaped basidiocarps which rarely exceed 2 mm in length and diameter (Bodensteiner *et al.* 2004). At the other end of the spectrum are species such as *Phellinus ellipsoideus*, which is responsible for producing the largest fruiting body ever recorded, weighing between 400 and 500 kg (Dai & Cui 2011). *Agaricomycetes* can also claim to contain some of the largest and oldest organisms on earth. In 1992, a genetically stable individual *Armillaria gallica* was shown to cover 15 hectares, weigh upwards of 10 000 kg and was aged at 1 500 yr old (Smith *et al.* 1992). In 2000, an individual colony of *Armillaria ostoyae* was identified in Oregon which was said to cover an incredible 965

hectares and estimated to be between 1 900 and 8 650 yr old (Ferguson *et al.* 2003).

In addition to being morphologically varied, agaricomycetes fill a wide range of ecological niches. A very large number of species are wood-decay fungi, which play a vital role in carbon cycling. Other species function as symbiotic partners, including symbionts of insects (Aanen *et al.* 2002, Mueller *et al.* 2005), but most notably as mycorrhizal plant-symbionts, which are essential for the survival of many plant species (Kohler *et al.* 2015). There are also parasitic and pathogenic agaricomycete species, with pathogens of timber and crop species being of particular importance (Brazee & Wick 2009, Farid *et al.* 2009). Human pathogenic fungi are generally limited to the ascomycetes, although *Schizophyllum commune* has been known to cause serious lung infections (Chowdhary *et al.* 2013). Although less common, agaricomycete species are increasingly being discovered in a variety of freshwater (Frank *et al.* 2010), marine (Hibbett & Binder 2001, Binder *et al.* 2006, Amend *et al.* 2012) and mangrove environments (Baltazar *et al.* 2009). Recently a new aquatic species of gilled mushroom belonging to the genus *Psathyrella* has been identified, which produces completely submerged fruiting bodies (Frank *et al.* 2010).

The ecological roles of agaricomycetes make them important within human societies due to the roles they play in industries such as forestry and agriculture, but they also impact us more directly, as a valuable source of nutrients and as medicinally relevant species. The vast majority of edible fungi are agaricomycetes, with the exception of the truffles and morels, which are ascomycete species. The most toxic fungi are also agaricomycetes however, such as the death cap, *Amanita phalloides*, which is responsible for the majority of fatal mushroom poisonings (Litten 1975).

Despite the relatively conspicuous nature of agaricomycete species and their relevance to human societies, they have not always garnered as much attention within the scientific community as other fungi, largely due to the relative difficulty in growing and studying them within laboratory settings. However, with the advent of modern molecular techniques, such as transformation systems and next generation sequencing, this fascinating and indispensable group of organisms are now becoming more and more accessible, and therefore the ways in which they can be exploited for human endeavours is increasing greatly.

This review will attempt to give an overarching perspective of the importance of the *Agaricomycetes*, by focusing upon selected species which we feel are representative of the main roles these fungi play within natural ecosystems and in the context of serving a particular purpose to human societies: as model species, as edible species, as decomposers, as toxic species, as medicinal mushrooms, as symbionts and as pathogens.

MODEL AGARICOMYCETES

The in-depth study of model species within all Kingdoms serves to deepen our understanding of the key biological processes shared by all life-forms, including evolution, genetics, cell biology, meiosis and pathogenesis. Fungi play a unique role in understanding such broad biological themes, sitting as they do between plants and animals in the tree of life, and in fact being more closely related to animals than plants, with the Fungi and Animalia Kingdoms being part of a monophyletic clade (Baldauf & Palmer 1993).

Being well understood and genetically tractable, model species not only inform our general understanding of life, but also serve as the foundation for extended research into the biology of other related species. As previously mentioned, one factor that has hampered the study of basidiomycetes has been the relative difficulty in studying these organisms in laboratory conditions. Therefore, detailed and systematic investigations into model species, and the subsequent development of molecular tools specifically adapted for basidiomycetes, have been vital in making the phylum as a whole more accessible.

This review will consider two model agaricomycetes: *Coprinopsis cinerea* and *Schizophyllum commune*. Both species have been studied in great detail, with thousands of peer-reviewed papers published elucidating key aspects of basidiomycete biology and describing the development of tools and techniques applicable to such species. This resulting body of knowledge has formed the basis of much of our understanding of this fascinating phylum.

Coprinopsis cinerea

Coprinopsis cinerea (Fig. 1A), commonly known as the “gray shag”, is a model multicellular basidiomycete (Redhead et al. 2001), which has been studied extensively. In nature, *C. cinerea* is found globally where it employs a saprotrophic lifestyle, favouring habitats containing dung and compost (Kjalke et al. 1992, Kues 2000). *Coprinopsis cinerea* is a coprinoid mushroom, collectively known as the “inky caps”, due to the fact that their caps liquefy on maturation to aid the dispersal of

basidiospores. As deliquescence occurs from the bottom of the gills upwards, the edges of the cap curl to expose mature spores to wind currents for dispersal (Pukkila 2011). The coprinoid basidiomycetes are an excellent example of convergent evolution, as recent molecular analyses have demonstrated that although they share this common trait, they are not in fact all closely related in evolutionary terms (Redhead et al. 2001).

Much of *C. cinerea*'s value as a model species lies in the fact that it is easy to cultivate on petri dishes in the laboratory, where mating and the full life cycle can be completed in just two weeks. A suite of molecular tools have now been developed for *C. cinerea*, including an established transformation system (Binninger et al. 1987, Granado et al. 1997, Collins et al. 2010, Dörnte & Kues 2012), a selection of marker genes (Kilaru et al. 2009b), gene silencing methods (Namekawa et al. 2005, Wälti et al. 2006, Heneghan et al. 2007, Costa et al. 2008) and strains which have been engineered to allow targeted gene disruption, a technique which is generally not feasible for agaricomycetes (Nakazawa et al. 2011). The genome sequence for *C. cinerea* also became available in 2010, revealing a haploid genome size of 37.5 Mbp (Stajich et al. 2010). This relative ease of working with *C. cinerea* and the available tools means extensive research has been carried out on many fundamental aspects of the biology of this species.

For example, the sexual reproduction of *C. cinerea* has been studied in great detail. As is now known to be typical for basidiomycetes, *C. cinerea* has two distinct stages to its lifecycle: as a primary monokaryote (from the Greek, mono = one; karyos = kernel or nucleus), which contains only one haploid nucleus per cell, and as a fertile dikaryote which contains two nuclei per cell (Fig. 1B). Dikaryotic mycelium forms when two sexually compatible monokaryotic hyphae fuse in a process called plasmogamy (Kues 2000, Raudaskoski & Kothe 2010). Unlike in the lifecycle of many plants and animals, karyogamy (nuclear fusion to produce a diploid cell) does not occur immediately for basidiomycetes and instead the dikaryotic state, with two distinct haploid nuclei per cell, is stably maintained indefinitely. Dikaryotic tissues can generally be recognised due to their vigorous growth and the presence of clamp connections at the hyphal septa, which are specialised structures that elegantly maintain the presence of two distinct nuclei in each cell (Fig. 1C).

When the necessary genetic and environmental factors coincide, fruiting bodies will then form from the dikaryotic mycelia, differentiating into three main tissue types: gill, stalk and cap. This differentiation process is incredibly complex and occurs via a well-defined developmental process that requires light/dark cycles and takes approximately one week (Fig. 1D). It is on the external surfaces of the gills in the basidia that nuclear fusion then occurs, followed by meiosis, and finally, haploid basidiospore formation (Kues 2000). After release and dispersal, these basidiospores germinate to produce a monokaryotic mycelium, thus completing the sexual lifecycle. Like 90 % of basidiomycetes, *C. cinerea* is heterothallic, meaning that two different and compatible monokaryons are required for mating to produce fertile dikaryons that are capable of fruiting and producing sexual spores. The remaining 10 % of basidiomycetes are homothallic, meaning that their spores germinate to produce fertile mycelia capable of fruiting (Raper 1966). *Agaricus bisporus*, one of the species discussed later in this review, is an interesting example of a basidiomycete where different varieties employ different lifestyles, including homothallic and heterothallic.

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