KINGDOM FUNGI

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Summary

Kingdom Fungi contains a diverse group of organisms. The common characters among all true Fungi are the presence of chitin in the cell wall and in most species, the presence of zygotic meiosis (meiosis that occurs in the zygote). The best-known fungi include mushrooms, molds and yeasts. However, fungal growth exists in an incredible range of sizes, shapes and colors. Additionally, fungi have adapted to diverse ecological niches that have enabled these organisms to thrive in almost every habitat on the planet. The majority of fungi are saprobes, facilitating the break-down of organic matter and enabling the recycling of carbon and other nutrients essential for the development and growth of all known living organisms.

However, other species are parasitic on plants, animals or other fungi, or they form various symbiotic relationships with plants and animals. Due to their microscopic size, fungi are often overlooked and their role in nature and human life underestimated. Most estimates of fungal diversity indicate that there are at least 1.4 million species still to be discovered; therefore the systematics and classification of fungi will continue to change as scientists continue the important work of documenting fungal diversity. Today with the aid of molecular data, the main taxonomic units of Fungi are better resolved than ever before, and are currently divided into eight phyla.

The largest and the most morphologically variable phyla are Ascomycota and Basidiomycota, which form the crown radiation of Fungi known as the Dikarya. Other phyla include arbuscular mycorrhizal fungi (Glomeromycota); chytrids (Blastocladiomycota, Chytridiomycota, Neocallimastigomycota), which possess posteriorly inserted whiplash flagella; and a potentially polyphyletic group, Zygomycota. Another group, Microsporidia, a group of intracellular animal pathogens, has also been shown to belong to Fungi, but its position in relation to other members of the kingdom has yet to be resolved.

1. Introduction

There are more than 110000 species known today in the kingdom Fungi. Taking into consideration their “celebrity,” we may say that the “king” could be the well-known

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button mushroom and the "queen" may be the chanterelle. However, every proper kingdom needs to have a large enough court and enough citizens for it to function properly. Various predictions have been made for the number of species in the fungal kingdom and at least 1.4 million but perhaps as many as five million fungal species remain undescribed. Thus, by any estimate less than 10% of fungal species have been discovered and described by science, and an even smaller percentage of these have been studied extensively. Thus, there is a vast need for both additional research and greater numbers of scientists trained to study these organisms.

The branch of biology devoted to the study of fungi is known as mycology, derived from the Greek word for "mushroom" – *Mykes*. Although the number of mycologists and fungal biologists today is greater than ever, the majority of these specialize on a small number of taxa, often "model fungi," leaving the majority of fungal groups understudied.

The best known fungi are probably the mushrooms that decorate parks and forest floors or our dinner plates. But mushroom-forming species are only a small part of the fungal kingdom, and most species are actually microscopic, growing for instance inside the plants in the garden or on the hair of the cat sitting on the street corner. Fungi surround us all on a daily basis and directly facilitate life on Earth by recycling important nutrients, serving as a food source for various organisms and facilitating the growth of plants. Of course, not all fungi are beneficial and many of them cause diseases in plants and animals and produce harmful toxins. Therefore, mycological research is very important for discovering new ways to benefit from fungi as well as to protect our food and health from fungal disease.

In this chapter we provide an overview of the general characteristics of fungi and their importance, review the current state of fungal systematics and genomics, and, finally, discuss each of the major groups of fungi. While classifications for these organisms have, and will continue to change, the importance of the members of this kingdom to humans and their impact on the world around us will not.

1.1. Importance of Fungi

1.1.1. Human Use of Fungi

Humans have used fungi on a daily basis since recorded time and beyond. Mushrooms and other fungal fruiting bodies have been used as a food source, in medicine, or as an aid in contacting spirits. For instance, in 1991 the well-preserved body of a bronze-age man, nicknamed the Iceman, was discovered in the Alps. Also preserved were his clothing, gear, and two species of fungi that he carried with him. One of these, *Piptoporus betulinus*, is believed to have been used for medical purposes, while the other, *Fomes fomentarius*, was used as fire tinder. The fact that these fungi were carefully tended and stored by the Iceman shows that they must have served an important role in the life of humans more than 5000 years ago. In fact fungi are still used in folk medicine in the Alps region today. Even earlier uses of fungi include the production of wine, beer and bread by ancient Egyptians and other cultures. The fermentative processes needed for the production of these foods are facilitated by

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microscopic fungi that were skillfully, although unknowingly, cultured at least 8000 years ago. Ancient writings contain descriptions of various fungal crop diseases that have plagued man since the beginning of agriculture, and gods, such as Robigus, the Roman god of rust and mildew, were invoked for protection against devastating epidemics.

In many ways, the use of fungi by modern man is similar to that in ancient times. The main use is in food production, where various foods are produced through fermentation (e.g. bread, alcoholic beverages, soy sauce, miso). Several edible mushrooms including the button mushroom (*Agaricus bisporus*) and shiitake (*Lentinula edodes*) are grown commercially and used on a daily basis, especially in Asian cuisine. Mycophagy of wild mushrooms, however, is probably practiced by fewer cultures than in the past, perhaps due to less knowledge about fungal species and their edibility by modern people. Fungi are also used in industry to produce various biochemical compounds, including antibiotics and other medically important products.

Some fungi are able to break down toxic compounds such as diesel fuel and phenol, and they contribute to bioremediation efforts to treat toxic waste or purify contaminated soils. Fungi can also serve as bio-indicators to detect changes in the environment. For example, some lichen species are especially sensitive to air pollution, while others can grow well in urban environments even with rather high pollution rates. Monitoring the occurrence of these lichens therefore provides information about the air quality. Additionally, fungi are utilized as natural fertilizers and as biological control agents to provide environmentally friendly pest or weed control in modern agricultural systems. Increasing issues with the use of artificial and chemically produced products and awareness about the need for sustainable systems will most likely result in the discovery of new uses of fungi.

1.1.2. Role in Nature

It is hard to over-emphasize the importance of fungi in the ecosystem functioning of the Earth. Fossils and molecular evidence indicate that fungi accompanied the first photosynthesizing organisms on land to help them cope with the harsh environment they met. Fungi were the first organisms to break down plant and other organic material and therefore facilitate the formation of soils.

Moreover, it has been speculated that fungi have greatly contributed to animal evolution by binding carbon and raising the atmospheric oxygen content, which enabled the development of large eukaryotic organisms in the oceans and led to the evolution of all animals we know today.

Even the extinction of dinosaurs and the subsequent rise of mammals have been proposed to have resulted from fungal infections that killed most of the cold-blooded animals. In this possible scenario, mammals survived because fungi were not able to grow in their higher body temperatures. Of monumental but often overlooked importance is the role that fungi play as the major decomposers of plant and animal material on the planet. Were the saprobic action of fungi to cease, the planet would

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become covered with debris, and nutrient recycling would be too slow for most of the life forms we know today to flourish or survive.

In modern ecosystems fungi play an important role in almost every nutrient cycle, either as sources of food, decomposers of organic materials, or essential symbionts of plants and animals, providing necessary nutrients or protecting their hosts. Although fungi are thought to be primarily terrestrial, recent studies have emphasized that a diversity of fungi are found in freshwater, seas and ocean bottoms, ranging from tropical to Arctic and Antarctic regions. Although the precise roles of fungi in these ecosystems are still poorly understood, it is clear that they are essential.

Therefore, studies of fungal diversity and conservation are important because as is the case with other organisms, fungi are becoming extinct due to the changes in the environment and as a result of human activities. Several countries have taken steps to protect fungi as is also done for animals, insects and plants, but only public awareness will make a real difference in the conservation and preservation of these organisms that helped to shape this planet and its ecosystems long before the advent of humans.

2. Fungal Biology

2.1. Somatic Growth

Fungi are eukaryotic (e.g., contain a nucleus) organisms, most of which grow as yeasts or as characteristic elongated cells called hyphae (Figure 1a, b). Yeasts are a unicellular growth form with a spherical to ovoid shape. They may be either colorless or pigmented and primarily grow in nutrient-rich and humid environments. Yeasts occur among zygomycetes (e.g., *Mucor*), ascomycetes (e.g. *Saccharomyces* spp.) and basidiomycetes (e.g. *Rhodotorula* spp.). Some yeasts, including several vertebrate pathogens (e.g., *Blastomyces*), also form hyphae at some stage of their growth.

Hyphae are long filamentous cells that are surrounded by a rigid cell wall. Fungal thalli (the fungal “body”) and a great variety of fruiting structures (e.g., mushrooms) are all produced by hyphae, which, when aggregated into groups are known collectively as mycelium (Figure 1c, l, m). Fungal cell walls contain chitin (more complex forms of chitin are also known from arthropods), glucans and mannose-containing glycoproteins. Hyphae can be septate, meaning that they are divided into numerous compartments or cells by internal cross-walls called septa (Fig 1a), or non-septate wherein the hyphae are multinucleate. The septa of most fungi have central pores that allow cytoplasm and organelles, sometimes including nuclei, to move from one cell to another, securing the transport of nutrients and necessary cellular components.

The structure of these septal pores is often an important character used to differentiate between fungal phyla and subphyla. An important characteristic of hyphae is that they grow apically in one direction only and often branch during growth. The rigid cell walls enable the build-up of turgor pressure inside the hyphae, allowing fungi to penetrate very dense tissues like plant epidermis or insect cuticles. The majority of fungi have no motile organs so they reach their food source by hyphal growth. Hyphal growth is also one method of dispersal and some fungi (e.g. *Armillaria ostoyae*) have reached several

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kilometers from their point of origin by spreading mostly in the soil as mycelium. Hyphae of some fungi may produce very dense structures called sclerotia (Figure 1c) that serve in overwintering as well as dissemination, showing that hyphae may serve various functions in the life cycle of fungi.

2.2. Asexual Reproduction

Most fungi produce asexual structures (Table 1). This reproductive strategy does not usually contribute to genetic diversity since all the spores produced are the result of mitosis (rather than meiosis, as in sexual spores) and are therefore genetically identical. However, asexual reproduction is advantageous in allowing the production of tremendous numbers of mitospores (spores produced by mitosis) that can be the main units of dissemination for a majority of species. There is an amazing diversity in form and mode of production of these spores in fungi.

The most commonly produced mitospores are called conidia (produced mainly by ascomycetes and some basidiomycetes), sporangiospores (produced by zygosporic fungi; Figure 1f), and zoospores (flagellated spores of chytrids; Figure 1e). Conidia and sporangiospores are usually formed on specialized hyphae called conidiophores or sporangiophores, respectively, that may be uni- or multicellular and vary greatly in size, shape and color. Asexually produced spores tend to be lighter and smaller than sexually produced spores and are therefore easily dispersed by wind, water or animals.

Fungi have developed many adaptations for mitospore dispersal in specialized niches such as the production of appendices and air pockets that help spores of non-motile aquatic species to ride on currents or float on foam; and the production of spores within a sticky sugary matrix, which attracts insects for dispersal. In addition, the flagellated zoospores of chytrids allow these propagules to swim to new substrates. Although very commonly found, not all fungi have known asexual stages, and especially in Agaricomycotina, reliance on this type of reproduction has been greatly reduced.

2.3. Sexual Reproduction

Sexual reproduction in fungi tends to be more infrequent than asexual reproduction and there is some evidence that, while long distance dispersal can occur, sexually produced spores are not as well adapted for this as asexually produced spores. Rather, meiospores (spores formed by meiosis) are increasing the genetic diversity of the populations by sexual recombination, and often are adapted for surviving harsh conditions (such as overwintering). One key feature that distinguishes Fungi from plants and animals is that the diploid condition in most species of Fungi is fleeting and often immediately followed by meiosis.

Thus, fungi are said to have zygotic meiosis. Sexual reproduction is typically initiated when haploid hyphae (or in some cases, haploid spores) from two compatible mating types fuse. What happens next varies greatly by fungal group, with the chytrids being especially variable, and will be discussed in more detail under the relevant sections in the following. In general, at some stage after plasmogamy, karyogamy and meiosis will occur within a specialized cell or structure that in ascomycetes is called an ascus

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(Figure1g), in basidiomycetes, a basidium (Figure 1h), and in zygomycetes, a zygosporangium. Meiospores are formed on or within these cells and are termed ascospores, basidiospores, and zygospores, respectively (Table 1).

Sexual reproduction in the chytrids is often, but not always, accomplished by the production of a resting sporangium (or resting spore) within which meiosis occurs. Not all fungi have known sexual reproductive stages.

In some cases, this stage may simply be rare and undiscovered, but in other cases the fungi may have lost their ability to reproduce sexually and are able to inhabit their niches successfully without the need for sexual recombination. Some fungi, especially within the Dikarya, produce elaborate fruiting bodies during this stage of development.

2.4. Metabolites

In addition to primary metabolites many fungi produce low-molecular-weight, often biologically active compounds known as secondary metabolites. Although these compounds may be chemically diverse, they are usually produced via common biosynthetic pathways, often related to morphological development.

Some secondary metabolites may have potent physiological activities that provide fungi with fitness benefits in nature, for instance, for competing with other microorganisms, for protection from consumption, for attracting a mate, or by facilitating their distribution by attracting vectors.

One example of vector attraction involves some gasteroid fungi (e.g. truffles) that form their fruiting bodies underground and have therefore no traditional means for spore dispersal.

However, their secondary metabolites are detected by various animals like pigs and squirrels, which dig out the fruiting bodies, eat them, and via their digestive system transport the fungal spores to new locations.

The best-known and most studied fungal metabolites are various toxins that harm vertebrates, including humans. For example the toxins of some *Amanita* species are lethal to humans within days after consumption, whereas other toxins, like those produced by *Aspergillus flavus* and ergot alkaloids produced by *Claviceps purpurea*, cause effects in humans after a longer period of consumption, sometimes months or even years.

The metabolites of other fungi such as certain species of *Psilocybe* may cause hallucinations when consumed and have been used not only recreationally but also for spiritual experiences. Other fungi have been shown to produce beneficial compounds such as antibiotics (e.g. *Penicillium* spp.), inhibitors of virus reproduction, and inhibitors of cancer cell growth (e.g. metabolites of *Ganoderma lucidum*). At present, numerous studies are aimed at uncovering new fungal secondary compounds of benefit to humans.

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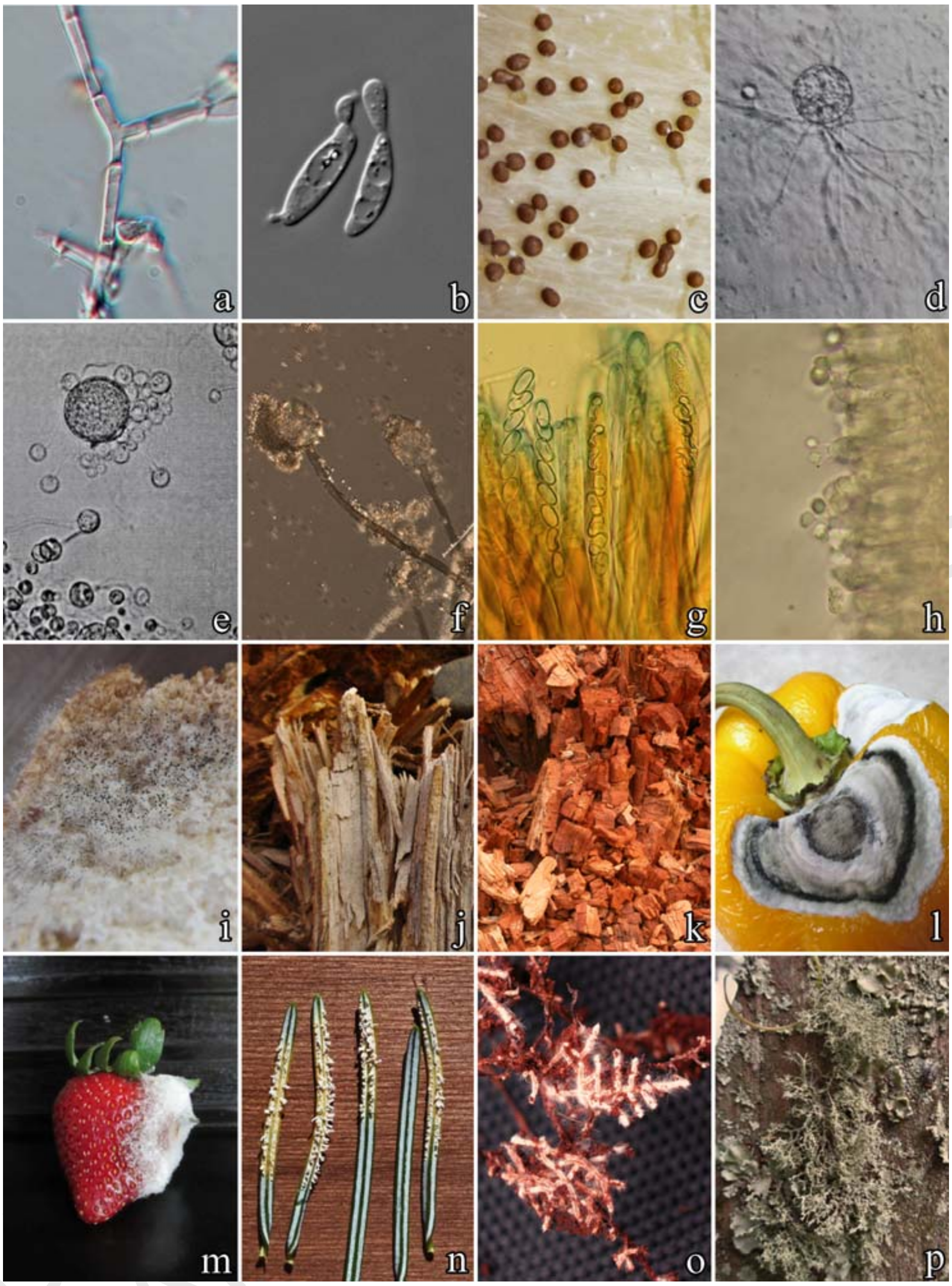

Figure 1. General features of Fungi.

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