BASIC MICROBIOLOGY

EDITOR: J.F. WILKINSON

VOLUME 7

Introduction to Modern Mycology

J.W. DEACON

SECOND EDITION

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Preface to second edition

In this second edition I have enlarged the text to provide greater depth of coverage of many topics and, where necessary, to update them. There is increased coverage of recent developments in plant pathology, fungicide resistance, insect pathology (which was not dealt with in the first edition) and I have especially emphasized the use of fungi in the biocontrol of insects and plant pathogens. There is also a new section on yeast plasmids, of use in genetic engineering.

In this I have been helped by the constructive criticisms of my colleagues, which I appreciate. I thank the many people who allowed me to reproduce drawings and photographs, acknowledged in the captions.

J.W.D.

October 1983

Preface to first edition

This undergraduate text on the biology of fungi is intended to appeal to microbiologists, botanists and biologists in general. Emphasis is placed on the characteristic or peculiar features of fungi, to show how fungi differ from other organisms and why they have attracted attention both from a fundamental viewpoint and from a practical one. The early chapters deal with major aspects of fungal growth, physiology and development; the later chapters then consider these in relation to the activities of fungi in nature – as agents of plant and animal disease, decomposition, etc. I have tried to include many of the most rapidly advancing areas of mycology, and have done so at the expense of some more traditional (but nevertheless worthy) areas, which are more than adequately covered in other texts.

I am pleased to thank Denis Garrett and Noel Robertson, who did much to foster my interest in fungi, and all those who provided material or ideas for inclusion in the book. I thank my family and friends for their patience, and Mrs J. Moseley and N. Thompson for typing from the manuscript. Lastly, I would be pleased to receive suggestions for improvement of the text, and to provide materials or advice, if possible, for teaching programmes.

Contents

1 Introduction

The aim of this book is to present an overall view of the activities of fungi, for both the microbiologist and the botanist. After this introductory chapter which contains an outline of fungal taxonomy, the book is divided into two main parts. The first presents the major aspects of fungal growth and physiology and includes a discussion of fungal biotechnology. The second presents the main activities of fungi in natural and agricultural environments. Finally, a chapter is devoted to the various ways of preventing and controlling fungal growth, since this presents a major challenge in modern mycology.

THE FUNGI: TOWARDS A DEFINITION

It is difficult to define the fungi in simple terms because several unusual organisms as well as the typical fungi are often included in this blanket term. Nevertheless, the typical fungi have a range of features that separate them from other organisms and which can be outlined here.

Fungi are typically filamentous. The individual filaments are termed **hyphae** (sing. **hypha**) and are surrounded by a wall which often, although not always, contains **chitin** as a major component. The hyphae grow only at their tips, so fungi exhibit **apical growth**, and they branch periodically behind the tips, the resulting network of hyphae being termed the **mycelium** (Fig. 1.1).

All fungi are **heterotrophs** (chemo-organotrophs): they require preformed organic materials which serve as both the energy source and as carbon-skeletons for cellular synthesis. Because of the rigid cell wall they cannot engulf food; rather they absorb simple soluble nutrients, which may be obtained from complex polymers by releasing extracellular enzymes (**depolymerases**) into the environment.

Fungi are **eukaryotic**, in contrast to the prokaryotic bacteria. In other words, they have discrete membrane-bound nuclei and a range of membrane-bound organelles, and their ribosomes are of the 80S type in contrast to the 70S type of bacteria (these terms referring to the sedimentation rate in a density gradient but, of more relevance, the types of ribosome are affected by different antibiotics, Chapter 14).

Fungi reproduce by both sexual and asexual means, but in either case they usually produce **spores** as the end-product. Spores differ greatly in size and shape, but are fundamentally different from the seeds of green plants because they do not contain a preformed embryo.

We shall see exceptions to some of these general points—especially in relation to filamentous growth, presence of a wall and the mode of nutrition. However, for now we can define the fungi—albeit in somewhat indigestible terms—as *eukaryotic, characteristically mycelial, heterotrophs with absorptive nutrition.*

RANGE OF FORM IN FUNGI

Although most fungi are mycelial and are colloquially termed 'moulds', there are three main exceptions to this rule. (1) Some fungi exist as **yeasts**, either budding off daughter cells (e.g., baker's yeast, *Saccharomyces cerevisiae*) or dividing by binary fission (e.g., *Schizosaccharomyces pombe*) (Fig. 1.1). These are true fungi, not fundamentally different from mycelial forms. Indeed, a few fungi can convert from a mycelial to a yeast form and vice-versa in response to environmental changes, and these **dimorphic** fungi (with two shapes) include some pathogens of man, being mycelial at 20–25°C and yeast-like at 37°C (Chapter 4). (2) Some of the lower fungi of the class **Chytridiomycetes** exist as single, large rounded cells or primitively branched chains of cells, which may be attached to the food source by tapering **rhizoids** (Fig. 1.1). (3) Some atypical fungi are grouped as the 'slime moulds'. They lack cell walls and often engulf food by phagocytosis; they are

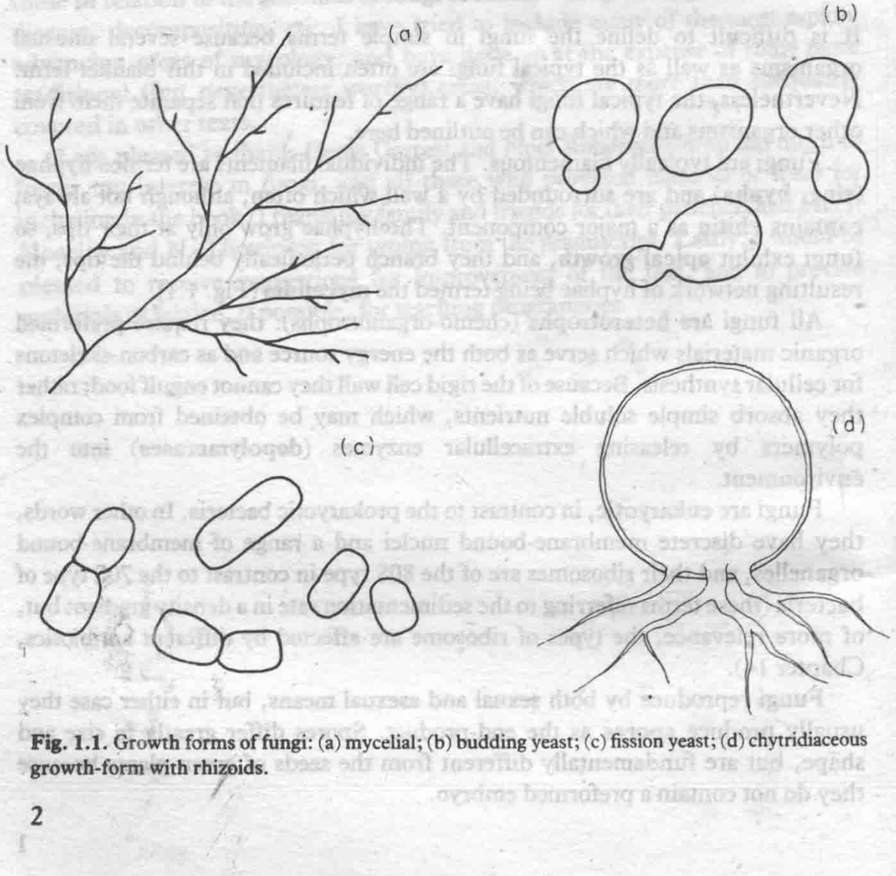

Fig. 1.1. Growth forms of fungi: (a) mycelial; (b) budding yeast; (c) fission yeast; (d) chytridiaceous growth-form with rhizoids.

similar in many respects to protozoa and perhaps, in some cases, are most appropriately classified with the lower animals.

With these exceptions, fungi have evidently found the mycelial growth form to be most advantageous, and the main differences in their vegetative stages are seen not in cell shape but in physiological features. Turning to reproductive structures, however, there is enormous variation in the size and shape of the spores and in the ways in which these are borne on the hyphae. These are not cosmetic differences; rather they are intimately linked with the specific needs of different fungi to disperse themselves to appropriate new environments (Chapter 9).

RANGE OF ACTIVITIES OF FUNGI

All heterotrophs ultimately depend on autotrophs like green plants for their energy sources, and in the case of fungi the same materials usually serve as carbon nutrients. If the food is obtained directly from another organism (the **host**) then the fungus can be termed a **parasite**; alternatively the fungus can be a **saprophyte** (**saprotroph**), obtaining food from dead organic material. It is appropriate to consider these separately.

Parasitism

Fungi are ideally adapted to parasitize plants, because the hyphal tips can penetrate even the intact plant surface and can then invade the internal tissues. If the parasite causes overt disease it is termed a **pathogen**, and fungal pathogens cause about 70 per cent of all the major crop diseases. For example, the potato blight fungus, *Phytophthora infestans*, caused devastating losses of potato crops in Ireland in the 1840s, with the result that an estimated one million people died of starvation and at least the same number emigrated to the rest of Europe and the USA. In the more recent Great Bengal Famine (1943), an estimated two million people died of starvation because of a severe outbreak of *Helminthosporium oryzae* on the rice crops. These are unusual and spectacular examples, but they merely illustrate the general importance of fungi as plant disease agents, which is discussed further in Chapter 12. However, not all parasites are detrimental—some are beneficial. In fact, nearly all higher plants in almost all environments have parasitic fungi living in association with their roots; these fungi form several types of **mycorrhiza** (Chapter 12) and they greatly increase the efficiency of mineral nutrient uptake from soil.

Some fungi parasitize other fungi (**mycoparasites**, Chapter 11), some parasitize insects (**entomogenous fungi**, Chapter 13) and some parasitize nematodes. The number of fungi involved in each case is relatively small. Nevertheless, they are important in terms of their specific adaptations and because they may act as natural population regulators. Some of these fungi are now used as commercial control agents in **biological control** programmes, as discussed in Chapters 13 and 14. Again, the penetrating ability of the hyphal tip—the 'invasive power' of hyphae—is important in these types of parasitism.

In contrast to plant diseases, fungi cause relatively few diseases of man and other warm-blooded animals. The **dermatophytes** or 'ringworm fungi' grow on the skin, nails and hair and cause the common but seldom serious diseases like athlete's foot and head ringworm. A few fungi cause internal, deep-seated mycoses of man, usually after entering the body via the lungs when spores are inhaled. Such diseases, although rare, pose a significant threat to compromised hosts, such as diabetics and people with a deficient immune defence system. These are discussed further in Chapter 13. Here we can note that several of these fungi grow as yeasts or equivalent single cells in the host, presumably because a unicellular phase is most appropriate for dispersal in circulating fluids in the body.

Saprophytism

Fungal saprophytes (Greek: *sapros*, rotten; *phuō*, grow) are important in almost all natural and man-made environments. There is probably no naturally-occurring organic material that cannot be degraded by one fungus or another, and the penetrating abilities of fungal hyphae enable them to degrade even complex structural materials like wood, insect cuticle etc. Fungi produce the major depolymerizing enzymes involved in cellulose and lignin breakdown (Chapters 5 and 10) and thus ensure the recycling of both carbon and mineral nutrients for continued plant growth. In addition, they produce some extremely complex and resistant polymers as a result of their saprophytic activities, these polymers being perhaps the main component of the **humic acid** fraction of soil humus, which contributes to soil fertility. Saprophytic activity of the type just described is usually termed **biodegradation** and it is essential in the biosphere. In addition, the fungi cause **biodeterioration**—an undesirable feature from the viewpoint of man because it results in many millions of pounds worth of damage to natural or artificial products. Thus, the fungi cause food spoilage, they rot wood, leather and fabrics, they grow on bathroom and kitchen walls, they grow on art treasures and they are a significant problem in lubricants etc. in manufacturing industries (Walters & Hueck-van der Plas 1972; Rose 1981). Sometimes the degradative activities as such are less important than the side-effects of fungal growth. For example, some food-spoilage fungi produce potent **mycotoxins** like the aflatoxins (Chapter 6) which render the food unusable; the aflatoxins are suspected as a cause of liver cancer in man and have certainly been shown to cause hepatomas in experimental animals. In a different context, the fungus *Amorphotheca resinae* is commonly found growing in aviation kerosene and, by its activities, it causes corrosion of the **aluminium walls** of aircraft fuel tanks (Chapter 5); it is a particularly difficult organism to control in practice, as discussed in Chapter 14.

EXPLOITATION OF FUNGI: BIOTECHNOLOGY

Fungi are used directly as food (as mushroom crops) and indirectly in beer-, wine- and bread-making (*Saccharomyces cerevisiae* or closely-related species). In addition, 'blue' cheeses are produced by inoculating *Penicillium roquefortii* into the veins, and various soft cheeses like camembert are produced by inoculation with *Penicillium camemberti*. This fungus grows on the surface of the cheese, producing a protease which breaks down the cheese structure. Less well-known, perhaps, is the use of fungi to produce soy sauce and to ferment many staple foods in Third World countries, upgrading an otherwise inadequate natural food. For example, soybeans are a very high-yielding and protein-rich crop, but much of the protein is unavailable in the diet because it is associated with fats and with a trypsin inhibitor. These problems can be overcome by inoculating cooked soybeans with the fungus *Rhizopus oligosporus* and incubating the material for 20–24 h at 30°C. The resulting product, **tempeh**, is highly nutritious and has a much-improved flavour; it is part of the staple diet of people in Indonesian villages, where the process has been operated for many years. Similarly, the fermented food product, **gari**, forms the staple diet of more than 30 million people in southern Nigeria; it is produced from the high-yielding root crop, **cassava**, better-known to most of us in its processed form, tapioca. Raw cassava contains an extremely toxic cyanogenic glycoside termed *linamarin*, but this is removed during the prolonged and largely uncontrolled fermentation practised in village communities. The fermentation is complex, but significant roles are played by the lactic acid bacteria, by *Corynebacterium* and by the yeast *Geotrichum candidum*, which gives the product its desired flavour (Ekundayo 1980).

Turning to more recent technological developments, there is increasing interest in the production of *single cell protein* (SCP) from fungi, either as a food for man or as an animal feedstuff. Extensive feeding trials have been conducted with the food yeast *Candida utilis*, and dried yeast (*Saccharomyces cerevisiae*) is already added to bread at a rate of 1 per cent to supplement this staple food. The main obstacle to further development is 'consumer resistance' to microbial foods. Nevertheless, several fungi are currently at the commercial or near-commercial stage of SCP production. They include *Fusarium graminearum* (Rank-Hovis-MacDougal in Britain), *Paecilomyces* sp. in the 'Pekilo process' in Finland, where the fungus is grown as an animal feedstuff on sulphite liquor from the wood pulping industry, and several yeasts (*Candida*, *Saccharomyces*, *Hansenula* and *Kluyveromyces*). Apart from sulphite liquor, the main substrates for SCP production include whey, paraffins, methanol and ethanol.

Chemical activities

In addition to food production, fungi are used in several important industrial processes. The main method of citric acid production for soft drinks etc. is based on growth of *Aspergillus niger* on sugars; the organic acid accumulates as a by-product of fungal metabolism, and current production world-wide is estimated to be about 300 000 tons per annum. Other organic acids like itaconic, gluconic, fumaric and malic acids are produced (or can be produced) by fungal fermentations.

The discovery of **penicillins** as products of *Penicillium notatum* literally changed the course of modern medicine. Today the penicillins are produced commercially by the closely-related fungus *Penicillium chrysogenum*, and they are structurally altered by chemical means, as described in Chapter 6. Other notable antibiotics of fungal origin include the **cephalosporins** and **griseofulvin**, but, as shown in Table 1.1, only a very few of the total number of antibiotics produced by fungi and other microorganisms have found important uses in chemotherapy. The antibiotics are typical of the compounds termed **secondary metabolites**—compounds that accumulate in microbial cultures at the end of the active phase of growth (Chapter 3). The plant hormones, **gibberellins**, are another group of secondary metabolites produced commercially from fungi, for the horticultural industry.

Table 1.1. Production of commercially important antibiotics. Adapted from Bérdy (1974).

Group of organisms	Total no. antibiotics produced	No. used commercially
Fungi	772	8
Bacteria—Actinomycetes	2078	72
—Others	372	10
Green plants and animals	854	0

Useful antibiotics of fungal origin*	Produced by	Active against	Site of action
Penicillins	*Penicillium chrysogenum*	Gram positive bacteria Gram negative bacteria	Wall synthesis
Cephalosporins	***Cephalosporium*** sp.	Gram positive bacteria	Wall synthesis
Griseofulvin	*Penicillium griseofulvum*	Most fungi	Mitotic spindle
Fusidic acid	*Fusidium coccineum* *Mucor ramannianus*	Gram positive bacteria	Ribosome

*Others include: Variotin from *Paecilomyces varioti*; Fumagillin from *Aspergillus fumigatus*; Siccanin from *Helminthosporium siccans*; and Xanthocillin from *Penicillium notatum*.

Finally, in this section, mention should be made of fungal enzymes, several of which are now commercially produced, although about 95 per cent of the total enzyme production by fungi comes from one fungus, *Aspergillus niger*. The four main fungal enzymes in commercial use are **α-amylase, amyloglucosidase, pectinases** and **proteases**. The α-amylase is used to convert starch to maltose and maltotriose in bread-making and is used in conjunction with amyloglucosidase to obtain glucose and maltose in 'high conversion' syrups based on maize and other starchy materials. The pectinases are used to clarify fruit juices and wines; their roles are detailed in Chapter 12. A specific acid protease from *Mucor meihei* is used as a rennin substitute to coagulate milk for cheese-making. Many more applications of fungal enzymes can be envisaged for the future; the great advantages of enzymes lie, of course, in their specificities, and the main disadvantages relate to their costs. In this respect, a significant recent advance has been made by immobilizing enzymes onto solid 'supports', so that the enzymes are recoverable from reaction mixtures or can be used as reactor beds through which liquids can be percolated to achieve the desired chemical conversions.

CLASSIFICATION OF FUNGI

The exact position of fungi relative to other organisms is a subject of much debate, which need not concern us here. Suffice to say that fungi have traditionally been considered as a subkingdom of the Plant Kingdom, but there are strong arguments for regarding them as a separate kingdom, equivalent to plants and animals (Whittaker 1969). In behavioural terms they have been described as animals that crawl about in tubes! Whatever their status, it is convenient firstly to distinguish between the wall-less fungi (**Myxomycota**) and the true walled fungi (**Eumycota**), as shown in Table 1.2, and then to divide the walled fungi into five

Table 1.2. Outline classification of fungi. Based on Ainsworth (1973). (Only the most important classes are shown.)

MYXOMYCOTA (wall-less organisms)

A ACRASIOMYCETES (cellular slime moulds). Amoeboid organisms that aggregate to form a fungus-like fruiting body.

B HYDROMYXOMYCETES (net slime moulds). Spindle-shaped cells that migrate within a tubular network of extracellular polysaccharide.

C MYXOMYCETES (true slime moulds). Multinucleate protoplasmic mass (plasmodium) that engulfs food particles.

D PLASMODIOPHOROMYCETES (endoparasitic slime moulds). Small plasmodia parasitic in cells of algae, fungi and higher plants.

EUMYCOTA (true, walled fungi)

A MASTIGOMYCOTINA. Produce flagellate asexual spores (zoospores).
- (i) *Chytridiomycetes*. Unicellular or primitive chains of cells, sometimes attached to food-base by tapering rhizoids. Zoospores have a single posterior whiplash flagellum.
- (ii) *Oomycetes*. Mycelial, aseptate. Zoospores have 2 flagella: an anteriorly directed tinsel type and a posteriorly directed whiplash type.

B ZYGOMYCOTINA. Usually mycelial, aseptate; non-motile asexual spores formed in a sporangium.
- (i) *Zygomycetes*. Usually saprophytic.
- (ii) *Trichomycetes*. Usually parasitic in guts of arthropods.

C ASCOMYCOTINA. Septate mycelium or yeasts; asexual spores not formed in sporangium; sexual spores formed in an ascus.
- (i) *Hemiascomycetes*. Yeasts or mycelial; ascus is not enclosed in a fruiting body (ascocarp).
- (ii) *Euascomycetes*. Mycelial; asci enclosed in an ascocarp.

D DEUTEROMYCOTINA. Septate mycelium or yeasts; asexual spores as in Ascomycotina; sexual reproduction absent, rare or unknown.
- (i) *Blastomycetes*. Typically yeasts.
- (ii) *Hyphomycetes*. Mycelial; asexual spores (conidia) formed on simple hyphae or hyphal branches (conidiophores).
- (iii) *Coelomycetes*. Mycelial: asexual spores formed from conidiophores in flask-shaped structure (pycnidium) or on pad of tissue (acervulus).

E BASIDIOMYCOTINA. Septate mycelium or yeasts; asexual spores absent or as in Ascomycotina; sexual spores formed on a basidium.
- (i) *Teliomycetes*. No special fruiting body (basidiocarp) to enclose the basidia; parasitic on higher plants (rusts and smuts).
- (ii) *Hymenomycetes*. Basidiocarp is a toadstool or bracket on which the basidia are exposed.
- (iii) *Gasteromycetes*. Basidiocarps various, enclosing the basidia.

main groups, termed **Mastigomycotina**, **Zygomycotina**, **Ascomycotina**, **Basidiomycotina** and **Deuteromycotina** (Table 1.2). Features of the wall-less organisms are outlined on pp. 11–12 and in Fig. 1.2; little more will be said about them in the rest of this book, but detailed accounts can be found in Olive (1975), or in the predominantly taxonomic texts of Alexopoulos & Mims (1980) and Webster (1980). The main features of the other fungal groups are outlined on pp. 12–22 and in Figs 1.3–1.8. Detailed accounts of the individual fungal groups can be found in Ainsworth *et al.* (1973).

The group Mastigomycotina includes all fungi that produce motile, flagellate spores (**zoospores**) and that, by and large, require free water at some stage in their life-cycles. However, the Mastigomycotina is not a 'natural' taxonomic grouping, and we distinguish within it two main classes which are more natural, termed the **Chytridiomycetes** and the **Oomycetes**. They differ, among other things, in the number of flagella on their spores and in their wall compositions, the Oomycetes being unusual amongst fungi in having **cellulose** or a cellulose-like polymer in their walls, instead of chitin. Indeed, the Oomycetes differ from other major groups of fungi in so many fundamental respects that they probably have a different evolutionary origin (Chapter 6).

The group Zygomycotina does not have motile, flagellate spores but is similar to the Mastigomycotina in at least one major respect: the asexual spores are formed by *cytoplasmic cleavage* within a cell termed the **sporangium**. This is considered to be a primitive feature, the Mastigomycotina and Zygomycotina usually being grouped together as the 'lower fungi', and in some of the older texts they are termed 'phycomycetes'. Additional features shared by these lower fungi are the fact that their hyphae characteristically lack cross walls or **septa** (sing. **septum**) and their vegetative hyphae have little, if any, ability to **anastomose** or fuse with one another at points of contact—a common feature in the higher fungi.

The group Ascomycotina is typified by the development of sexual spores in a cell termed an **ascus**. The asexual spores are not formed in a sporangium but develop in various ways directly from the hyphae; they are termed **conidia** (sing. **conidium**). The Ascomycotina is clearly a natural taxonomic grouping, and it includes numerous mycelial fungi (with septa) as well as the majority of yeasts. In the latter case, the ascus is formed merely by the fusion of two compatible vegetative cells during sexual reproduction.

The group Deuteromycotina is appropriately considered next; it is used mainly for convenience to accommodate all those fungi that seldom, if ever, produce sexual stages. In all other respects, however, these fungi are similar to the Ascomycotina, and when sexual stages are discovered they are usually found to belong to the Ascomycotina. It is notable that many common and extremely successful fungi can exist without recourse to sexual reproduction; the reasons for this are discussed in detail in Chapter 8. For now, we must note that the Deuteromycotina present considerable problems in nomenclature. They are usually named according to the stages that we commonly see: the asexual or 'imperfect' stages termed **anamorphs**. The genera so-recognized are sometimes referred to as 'form-genera', ***Penicillium*** and ***Aspergillus*** being typical examples. If the sexual or 'perfect' stages, termed **teleomorphs**, are found then a proper name has to be applied to these, and the teleomorphic name should be used to replace the anamorphic name in such cases. Unfortunately, the different species of, for example, *Aspergillus* can have quite different sexual stages; in the case of *Aspergillus* they are placed in no less than nine different genera in the Ascomycotina. Therefore, it is impossible to abandon the anamorphic name unless there is a constant association between a particular anamorph and its teleomorphic stage. Even then, the anamorphic name is so firmly rooted in the literature and in common parlance that it tends to be retained. This potential confusion should not be over-emphasized, but it is introduced here in order to explain why we can have more than one name for a single fungus (Kendrick 1979). Some examples are shown in Table 1.3.

The group Basidiomycotina includes the toadstool-producers and fungi that form large bracket-shaped fruitbodies on wood, but it also includes two very common and important groups of plant pathogens, the **rusts** and the **smut** fungi, which are entirely microscopic. The features of the group include the production of sexual spores on a special cell termed the **basidium**, and asexual reproduction (where present) is by conidia or similar spores. There has been an unfortunate tendency for people to refer to some of these fungi as 'macrofungi' and for microbiologists, accordingly, to reject them as 'macroorganisms'. Let it be said that they are the most remarkable microorganisms: in order to disperse spores of microscopic proportions (about 5 μm diameter) from hyphae of similar microscopic proportions they have had to evolve, in several cases, fruitbodies equivalent to tower-blocks (Chapter 4).

From all the comments made so far, and from the details in Table 1.2 and on pp. 11–22, it will be clear that fungal taxonomy is based predominantly on *morphological* criteria and especially on the features of the sexual reproductive structures. Actually, it would be more accurate to say that taxonomy is based on the *developmental* features of these structures, as these are considered to be 'conservative' features, least subject to selection pressure and, thus, least subject

Table 1.3. Generic names of some asexual (anamorph) and sexual (teleomorph) stages of fungi discussed in the text.*

Anamorph	Teleomorph	Chapter reference
Aspergillus	*Eurotium* *Emericella*	1, 6, 7, 8
Penicillium	*Eupenicillium* *Talaromyces*	1, 6, 7, 8
Trichoderma *Cephalosporium*	*Hypocrea*	11
Fusarium	*Gibberella* *Nectria*	8, 10
Microsporum	*Nannizzia*	13
Trichophyton	*Arthroderma*	13
Rhizoctonia	*Ceratobasidium* (Basidiomycotina) *Thanatephorus* (Basidiomycotina)	10, 12

***The table shows that 'form-genera' based on asexual stages do not necessarily correspond to single 'true' genera based on sexual stages, or vice-versa.**

to convergent evolution. There has been no real need to develop alternative approaches to fungal taxonomy, such as analysis of base ratios in the DNA or analysis of the biochemical or physiological attributes, although these are important in the taxonomy of yeasts, as of bacteria, because yeasts provide few useful morphological features. A consequence is that, wherever possible, the main taxonomic groupings down to variety-level (below species-level) are based on some morphological difference from other fungi.

THE MAJOR GROUPS OF FUNGI

1. Myxomycota (slime moulds) (Fig. 1.2)

Four groups: Acrasiomycetes, Hydromyxomycetes, Myxomycetes and Plasmodiophoromycetes. All have wall-less vegetative stages.

Acrasiomycetes (cellular slime moulds)

Unicellular amoeboid organisms that engulf bacteria and other food particles. Common in moist soil, leaf litter, etc. In most members the amoebae aggregate to form a **pseudoplasmodium**, shown to occur in response to pulses of cyclic AMP in the most-studied member *Dictyosteleum discoideum.* The pseudoplasmodium produces a cellulosic stalk on top of which is a head of spores. The walled spores germinate to release amoebae.

Hydromyxomycetes (net slime moulds)

Naked spindle-shaped cells that glide in a tubular network of extracellular polysaccharide. Most species are parasitic in marine algae or higher plants. *Labyrinthula macrocystis* is apparently a damaging parasite of eel grass, *Zostera marina*; the other members are little known.

Myxomycetes (true slime moulds)

Consist of a naked multinucleate mass of protoplasm, the **plasmodium**, which engulfs food particles. Common in rotting wood, leaf litter, etc. Most species reproduce by forming a fruitbody (a **sporangium**) which contains walled, wind-dispersed spores. The spores germinate to produce amoebae which engulf food and divide by binary fission. The amoebae can produce flagella and function as **gametes** (sex cells), fusing with one another to form diploid **zygotes** which develop into plasmodia. The species *Physarum polycephalum* is intensively studied by morphogeneticists. Its bright yellow plasmodium shows one of the fastest known rates of cytoplasmic streaming, and in response to light and nutrient starvation the whole plasmodium converts into a mass of black sporangia.

Plasmodiophoromycetes (endoparasitic slime moulds)

'Obligate' parasites of higher plants, algae or fungi; they exist in the cells of

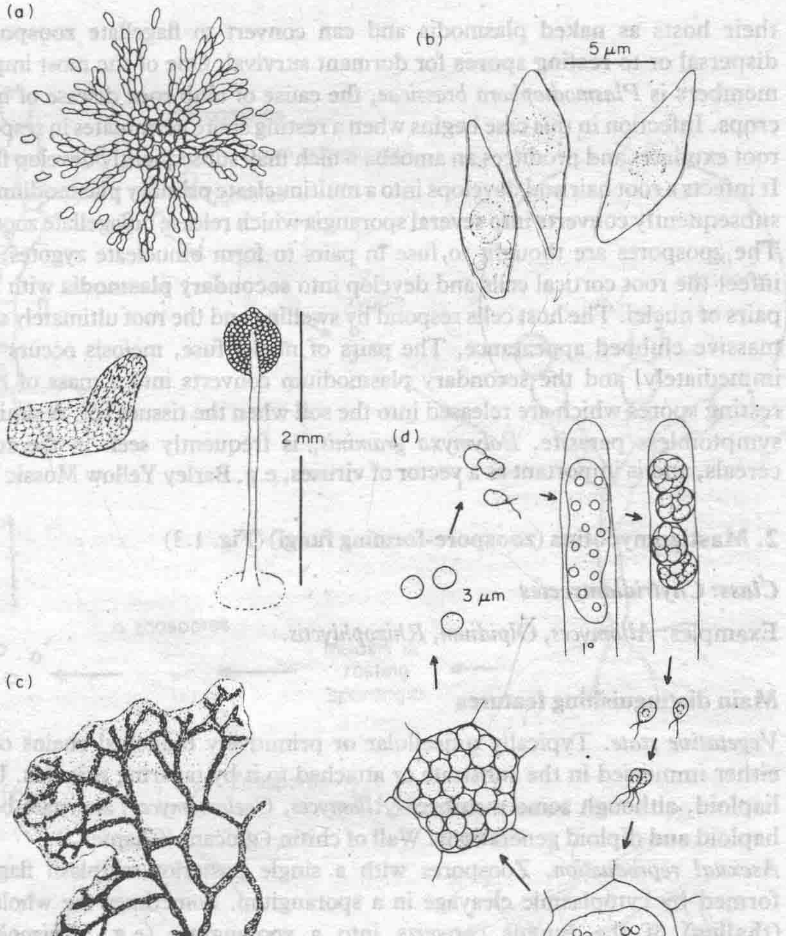

Fig. 1.2. Diagrammatic representation of Myxomycota. (a) *Dictyosteleum discoideum*, showing aggregation of amoebae, a pseudoplasmodium about to produce a fruitbody, and the stalked fruitbody. (b) *Labyrinthula macrocystis*, showing naked, spindle-shaped cells in 'slime filaments'. (c) *Physarum polycephalum*, showing part of a naked plasmodium in which the most rapid protoplasmic streaming occurs in the major channels. (d) *Plasmodiophora brassicae*, showing stages of development in root hairs (primary plasmodium (1°) and sporangia) and in root cortical cells (secondary plasmodium (2°) and resting spores). The intermediate phases (germination of resting spores and release of zoospores from sporangia) occur in the soil.