Basic Microbiology

EDITOR: J.F. WILKINSON

Volume 7
Introduction to Modern Mycology

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Preface

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.

J.W.D.

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. There are several excellent books that deal with fungal taxonomy, so only an outline of this will be presented here, later in this chapter; even so, this brief treatment is sufficient to understand the biology of fungi. After a general introduction the book is divided into two main sections. The first presents the major aspects of fungal physiology and growth; the second, the roles of fungi in the natural environment. Finally, a chapter is devoted to ways of controlling fungal growth, as this presents a major challenge in modern mycology.

THE FUNGI: A DEFINITION

It is almost impossible to define 'the fungi' in simple terms because several unusual organisms as well as the typical fungi are included in this blanket term. For this reason it is best to consider the main features of fungi and the ways they differ from other organisms before attempting a definition at the end of this chapter (p. 25). For now, we can note that fungi are characteristically filamentous, or thread-like. The individual threads are called **hyphae (sing. hypha)** and they branch profusely, often fusing with one another; this mass of branched hyphae is termed

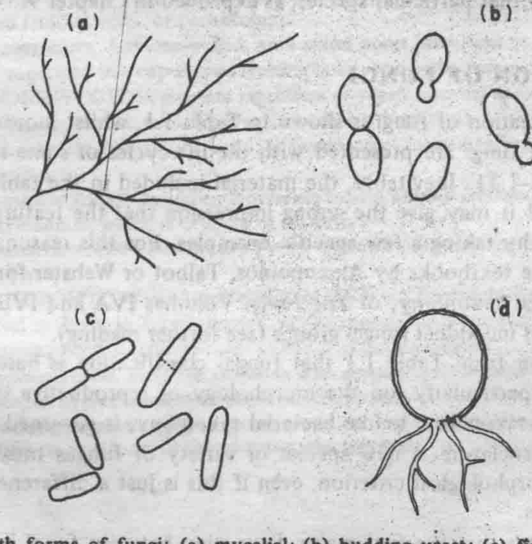

Fig. 1.1 Growth forms of fungi: (a) mycelial; (b) budding yeast; (c) fission yeast; (d) chytidriaceous growth form with rhizoids.

the mycelium (Fig. 1.1a). The individual hyphae are surrounded by rigid cell walls and grow only at their extreme tips. Indeed, this form of apical growth separates fungi from almost all other organisms–even filamentous ones. Fungi obtain energy from preformed organic compounds; the simplest of these, like monosaccharides and amino acids, are taken-up intact, but most must be degraded to simple monomers by means of extracellular enzymes before they are absorbed through the walls. Finally, fungi reproduce by both sexual and asexual means, but in either case they produce spores as the end-product; these vary greatly in shape and size but they are fundamentally different from the seeds of higher plants because they do not contain a pre-formed embryo.

RANGE OF FORM IN FUNGI

Fungi show little variation in their feeding stages–the vegetative or *somatic* stages. The vast majority are mycelial (Fig. 1.1a) and there are basically only three departures from this pattern. (1) Some exist for all or part of their lives in a yeast-like form (Fig. 1.1b and c), either budding-off daughter cells or dividing by binary fission. (2) Some lower fungi (Class: Chytridiomycetes) consist of a single rounded cell or branched chains of cells attached to the food source by tapering rhizoids (Fig. 1.1d). (3) Some of the lower fungi, the slime moulds, are wall-less organisms that engulf their food by phagocytosis (Fig. 1.2). With these exceptions, it seems that fungi have found the mycelial growth form to be most advantageous and the major differences between them are found in their physiologies.

Turning to reproductive structures, we see a quite different situation. Not only are the spores themselves very variable (Fig. 9.1), but also these are borne in a variety of ways (Figs 1.3-1.11). In each case, the shape and size of the spore and the organization of the spore-bearing structure is designed to facilitate dispersal to a suitable habitat for that particular species, as explained in Chapter 9.

CLASSIFICATION OF FUNGI

An outline classification of fungi is shown in Table 1.1, whilst more details of individual groups of fungi are presented with the life-cycles of some representative genera in Figs 1.2-1.11. Inevitably, the material included in the table and figures is incomplete, and it may give the wrong impression that the features of a group can be illustrated by taking a few specific examples. For this reason, readers may wish to consult the textbooks by Alexopoulos, Talbot or Webster for an extensive treatment of fungal taxonomy, or *The Fungi* Volumes IVA and IVB for comprehensive accounts of individual fungal groups (see further reading).

It will be seen from Table 1.1 that fungal classification is based largely on morphology and, particularly, on the morphology of reproductive structures. Indeed, since fungal taxonomy, unlike bacterial taxonomy, is governed by the Rules of Botanical Nomenclature, a new species or variety of fungus must differ from others in some morphological criterion, even if this is just a difference in size of a particular structure.

Table 1.1 shows that the first major distinction between fungi is made on the basis of presence or absence of a cell wall: wall-less fungi are grouped as the

Table 1.1 Outline classification of fungi. Based on G. C. Ainsworth (1973) *The Fungi, Volume IVA;* only the most important classes are listed.

1 MYXOMYCOTA (Wall-less forms)

1A ACRASIOMYCETES (cellular slime moulds). Usually amoeboid organisms that aggregate to form a fruiting body.

1B HYDROMYXOMYCETES (net slime moulds). Spindle-shaped cells with slimy filaments that join together to form a slimy network; mostly parasitic on marine plants.

1C MYXOMYCETES (true slime moulds). Consist of a multinucleate protoplasmic mass, the plasmodium.

1D PLASMODIOPHOROMYCETES (endoparasitic slime moulds). Small plasmodia parasitic within cells of fungi, algae or higher plants.

[1A and 1B are perhaps more appropriately considered as Protozoa, though they are studied by mycologists.]

2 EUMYCOTA (true, walled fungi)

2A MASTIGOMYCOTINA (produce flagellated spores (zoospores)).

(i) *Chytridiomycetes.* Vegetative state often unicellular; zoospores have single, posterior whiplash flagellum.

(ii) *Oomycetes.* Vegetative state usually mycelial (aseptate, i.e. no cross-walls); zoospores have two flagella, one directed backwards and one forwards.

2B ZYGOMYCOTINA (usually mycelial, aseptate; asexual spores non-motile, formed in a sporangium; sexual spore is a zygospore).

(i) *Zygomycetes*, usually saprophytic.

(ii) *Trichomycetes*, often parasitic on arthropods.

2C ASCOMYCOTINA (septate mycelium or yeasts; asexual spores non-motile, not formed in a sporangium; sexual spores formed in an ascus, usually within a fruiting body, or ascocarp).

(i) *Hemiascomycetes.* No fruiting body.

(ii) *Loculoascomycetes.* Two-walled ascus; fruiting body a stroma, or mass of tissue.

(iii) *Plectomycetes.* Asci one-walled, break down at maturity and typically contained in a closed fruiting body, or cleistothecium.

(iv) *Pyrenomycetes.* Asci one-walled, with apical pores or slits, contained within a flask-shaped fruiting body, or perithecium.

(v) *Discomycetes.* Asci one-walled, with apical pores, slits, caps or with no apical apparatus; contained in a cup-shaped fruiting body, or apothecium.

2D BASIDIOMYCOTINA (septate mycelium or yeasts; asexual spores absent or, when present, non-motile; sexual spores formed on a basidium).

(i) *Teliomycetes.* No fruiting body, or basidiocarp, formed to bear basidia; parasitic on higher plants.

(ii) *Hymenomycetes.* Basidiocarp present; basidia usually arranged in an organized layer, the hymenium, which is exposed at maturity.

(iii) '*Gasteromycetes*'. Basidiocarp present; basidia normally enclosed within this at maturity.

2E 'DEUTEROMYCOTINA' or 'FUNGI IMPERFECTI' (septate mycelium or yeasts; asexual spores as in Ascomycotina; sexual spores absent, rare or unknown).

(i) *Blastomycetes.* Budding single cells or a 'pseudomycelium'.

(ii) *Hyphomycetes.* Mycelial; sterile or with asexual spores borne directly on hyphae or on special hyphal branches termed conidiophores.

(iii) *Coelomycetes.* Mycelial; asexual spores formed in a flask-shaped structure (pycnidium) or on a 'pad' of fungal tissue, the acervulus.

Myxomycota (Fig. 1.2), though in some cases they are more akin to Protozoa than fungi; all walled fungi are grouped as the **Eumycota** (literally, 'true fungi'). The Eumycota are then divided into five main categories, here termed the **Mastigomycotina**, **Zygomycotina**, **Ascomycotina**, **Basidiomycotina** and **Deuteromycotina**. Of these, the Zygo-, Asco- and Basidio-mycotina seem to be 'natural', well-defined groupings in the taxonomic sense. But the Mastigomycotina is a composite grouping, covering all fungi that form motile, flagellated spores (**zoospores**). It contains, among others, two important but seemingly unrelated Classes, the **Chytridiomycetes** and **Oomycetes**; indeed, the Oomycetes may have a quite different evolutionary origin to that of most other fungi (Chapter 6). The Deuteromycotina is a totally unnatural grouping, being little more than a convenient pigeon-hole in which to place fungi whose sexual stages are rare, unknown or absent but which would otherwise normally fall in the Ascomycotina. For convenience—and sometimes of necessity—such fungi are classified according to their asexual ('imperfect') stages, but when sexual stages occur then each fungus must also be assigned a 'perfect' name. This leads to the anomaly that some fungi can have two quite different names, depending on the state in which they are found; some examples are shown opposite Fig. 1.11. These points are of some importance because an enormous number of common and industrially/environmentally important fungi fall within the Deuteromycotina; they include *Penicillium, Aspergillus, Fusarium* and many other so-called 'form-genera' rather than true genera. The reason why so many obviously successful fungi can exist without recourse to sexual reproduction, is interesting in itself and will be discussed in Chapter 8.

A final point of note is that there appears to be an evolutionary lineage running from the Mastigo- and Zygo-mycotina, through the Ascomycotina to the Basidiomycotina. The evidence for this is, of course, wholly deductive, and is based upon details of the morphology of specific—in some cases, obscure—fungi, so it cannot be considered here. We can note, however, that the Mastigo- and Zygo-mycotina are often referred to as the 'lower fungi', and that they have two gross features which separate them from the rest: (1) cross-walls, or *septa*, are usually absent from their hyphae (see p. 35); (2) their asexual spores are usually formed by cleavage of the cytoplasm within a cell, the *sporangium* (see p. 55).

Some of the many problems inherent in fungal taxonomy are illustrated by the disagreement between taxonomists. For example, while most authorities agree with the basic classification used here, they disagree on whether the fungi rank as a Kingdom, equivalent to plants and animals, or a Sub-Kingdom or Division of the Plant Kingdom. This is no trifling point to the everyday mycologist, for its effect is to shift all the major categories up or down one rank, from Sub-division down to Class or from Class down to Sub-class, etc. and hence to alter many of the names used! By convention, names of fungal Sub-divisions end in '-mycotina', those of Classes in '-mycetes', Orders in '-ales' and Families in '-aceae'.

Myxomycota (slime moulds)

Four classes: *Acrasiomycetes* (cellular slime moulds), *Hydromyxomycetes* (net slime moulds), *Myxomycetes* (true slime moulds), *Plasmodiophoromycetes* (endoparasitic slime moulds).

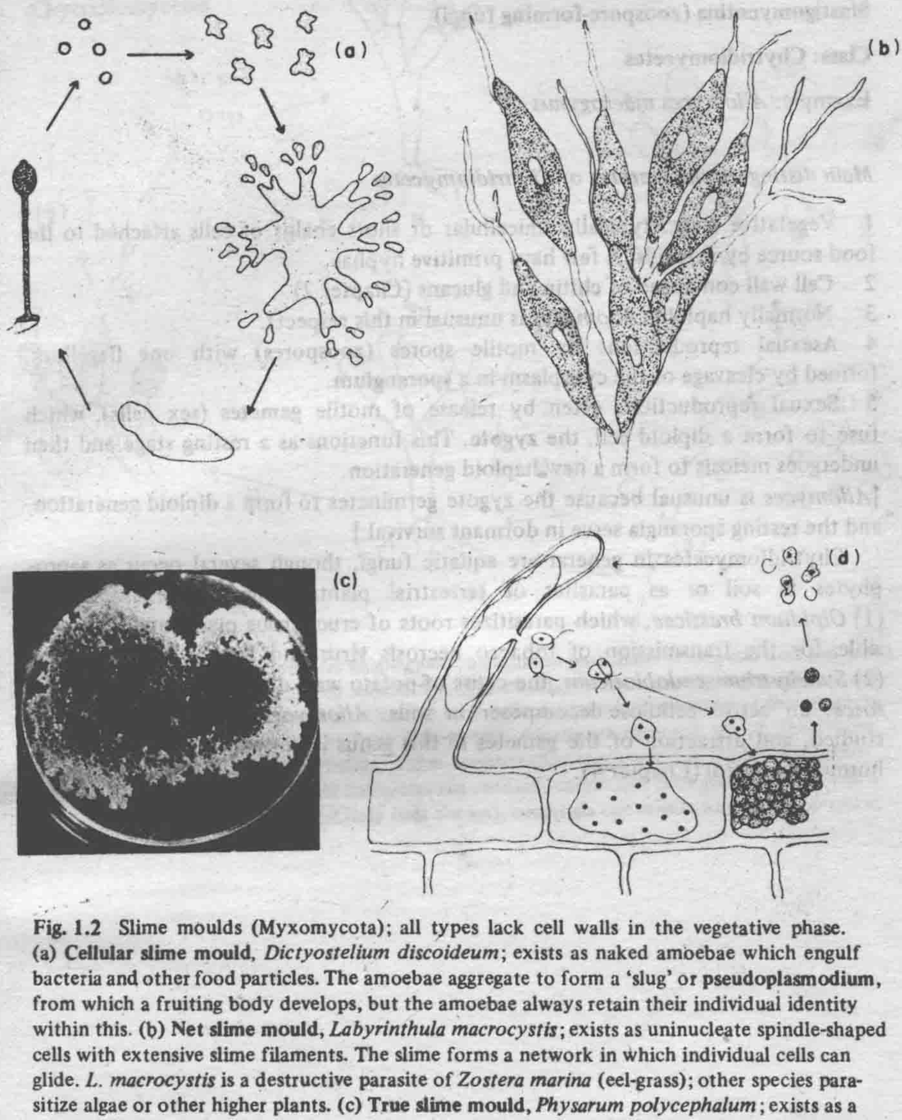

Fig. 1.2 Slime moulds (Myxomycota); all types lack cell walls in the vegetative phase. **(a) Cellular slime mould,** *Dictyostelium discoideum*; exists as naked amoebae which engulf bacteria and other food particles. The amoebae aggregate to form a 'slug' or **pseudoplasmodium,** from which a fruiting body develops, but the amoebae always retain their individual identity within this. **(b) Net slime mould,** *Labyrinthula macrocystis*; exists as uninucleate spindle-shaped cells with extensive slime filaments. The slime forms a network in which individual cells can glide. *L. macrocystis* is a destructive parasite of *Zostera marina* (eel-grass); other species parasitize algae or other higher plants. **(c) True slime mould,** *Physarum polycephalum*; exists as a multinucleate network of protoplasm, the **plasmodium,** which engulfs bacteria. Fruiting bodies which release dry powdery spores are formed in the autumn and are frequently seen on moist, rotting wood. ***P. polycephalum*** **is used extensively in morphogenetic studies; it requires light to initiate fruiting, shows chemotaxis (movement in response to chemical stimuli) and has the fastest known rate of cytoplasmic streaming. (d) Endoparasitic slime mould,** ***Plasmodiophora brassicae*; exists as a naked plasmodium within plant cells and causes the damaging 'clubroot' disease of cruciferous plants (Chapter 12).** ***P. brassicae*** **is released from the cells of the root cortex as resting spores (far right in Fig. 1.2d); these germinate to release amoebae which infect root hairs. Within a root hair the fungus forms a (primary) plasmodium, which is later converted into a zoosporangium and releases flagellate zoospores. The zoospores fuse to form binucleate zoospores; these become plasmodia, enter a root cortical cell and fuse with other**

Legend continues on p. 6

Mastigomycotina (zoospore-forming fungi)

Class: Chytridiomycetes

Example: *Allomyces macrogynus*.

Main distinguishing features of Chytridiomycetes

1 Vegetative state: typically unicellular or short chains of cells attached to the food-source by rhizoids. A few have primitive hyphae.
2 Cell wall composed of chitin and glucans (Chapter 2).
3 Normally haploid (*Allomyces* is unusual in this respect).
4 Asexual reproduction: by motile spores (**zoospores**) with one flagellum, formed by cleavage of the cytoplasm in a **sporangium**.
5 Sexual reproduction: often by release of motile **gametes** (sex cells), which fuse to form a diploid cell, the **zygote**. This functions as a resting stage and then undergoes meiosis to form a new haploid generation.
[*Allomyces* is unusual because the zygote germinates to form a diploid generation, and the resting sporangia serve in dormant survival.]

Chytridiomycetes in general are aquatic fungi, though several occur as saprophytes in soil or as parasites of terrestrial plants. Important examples are (1) *Olpidium brassicae*, which parasitizes roots of cruciferous plants and is responsible for the transmission of tobacco necrosis virus and lettuce big-vein virus; (2) *Synchytrium endobioticum*, the cause of potato wart disease; (3) *Rhizophlyctis rosea*, an active cellulose-decomposer in soils. *Allomyces* has been extensively studied, and attraction of the gametes in this genus is known to be under simple hormonal control (Chapter 4).

such plasmodia to form a large secondary plasmodium. Within this the nuclei fuse, meiosis occurs and resting spores are produced to repeat the cycle on another root hair. Other endoparasitic slime moulds include *Polymyxa graminis* (cereals and grasses), *Spongospora subterranea* (potatoes), and species that parasitize algae and fungi; none of these has been grown in the absence of its host.

Chytridiomycetes

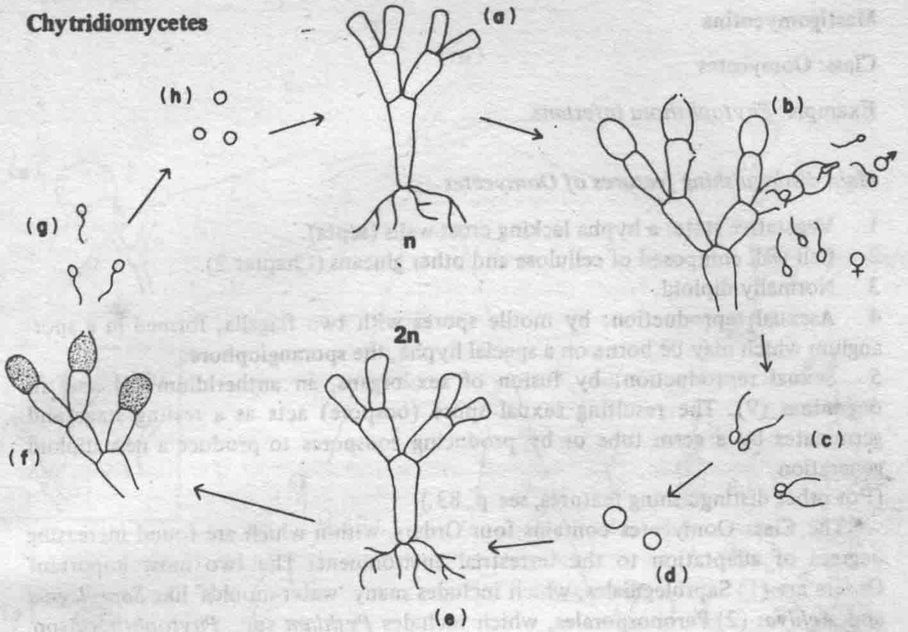

Fig. 1.3 Life cycle of *Allomyces macrogynus*, a common inhabitant of tropical soils and muds. (a) Vegetative thallus attached to substratum by rhizoids. (b) Sex organs (gametangia) are produced and release motile gametes (sex cells) by localized enzymic breakdown of the gametangium wall. (c)–(d) Gametes fuse to form diploid cells; flagella are retracted. (e)–(f) The zygote germinates to form a diploid thallus, which forms resting sporangia. (g)–(h) Meiosis occurs within resting sporangia; haploid zoospores are released, encyst and then germinate to form a new haploid generation. Alternatively (not shown), sporangia can release diploid zoospores at (f) to repeat the diploid phase.

Mastigomycotina

Class: Oomycetes

Example: *Phytophthora infestans.*

Main distinguishing features of Oomycetes

1 Vegetative state: a hypha lacking cross-walls (**septa**).
2 Cell wall composed of cellulose and other glucans (Chapter 2).
3 Normally diploid.
4 Asexual reproduction: by motile spores with two flagella, formed in a sporangium which may be borne on a special hypha, the **sporangiophore**.
5 Sexual reproduction: by fusion of sex organs, an **antheridium** (♂) and an **oogonium** (♀). The resulting sexual spore (**oospore**) acts as a resting stage and germinates by a germ tube or by producing zoospores to produce a new diploid generation.

(For other distinguishing features, see p. 83.)

The Class Oomycetes contains four Orders, within which are found increasing degrees of adaptation to the terrestrial environment. The two most important Orders are (1) **Saprolegniales**, which includes many 'water-moulds' like *Saprolegnia* and *Achlya*; (2) **Peronosporales**, which includes *Pythium* spp., *Phytophthora* spp. and the important 'downy mildew' parasites of higher plants. In the Saprolegniales and some of the Peronosporales the sporangia always remain attached to the parent hyphae and release zoospores; in higher members of the Peronosporales, by contrast, the sporangia become detached and wind-blown, and in a few cases like *Phytophthora* can germinate directly by means of germ tubes (see Chapter 4). One small Order, the *Leptomitales*, includes the only obligately fermentative fungus known to date (p. 92), and the species of this Order, in general, show interesting physiological differences from most other fungi (Chapter 5).

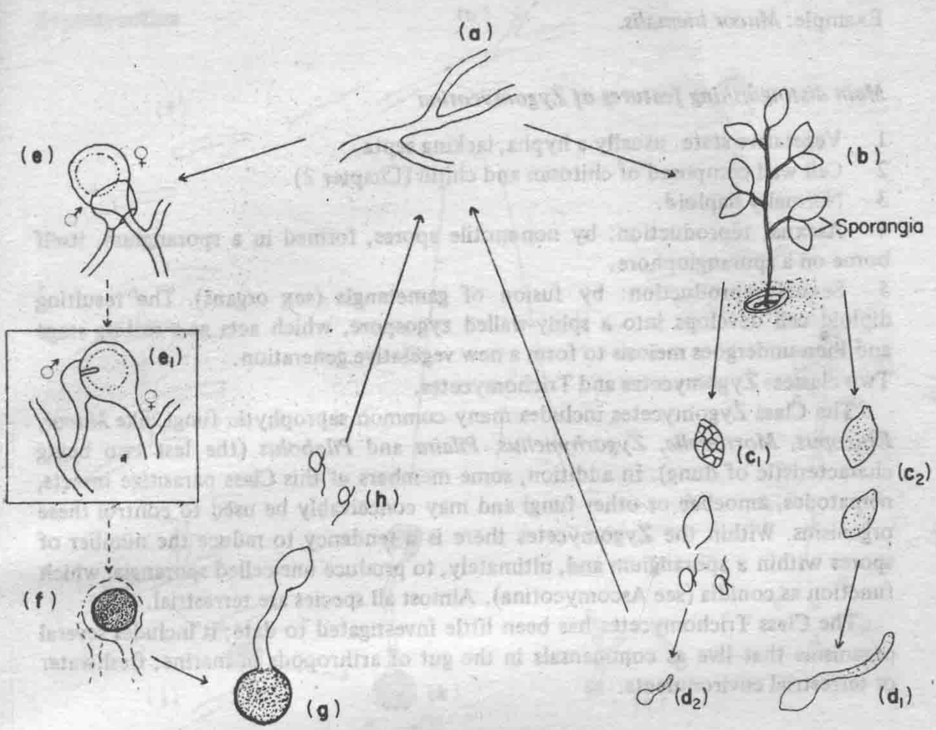

Fig. 1.4 Life cycle of *Phytophthora infestans*, the cause of potato blight. (a) Diploid vegetative mycelium within a plant. (b) Asexual reproduction occurs by production of sporangia, the sporangiophore projecting through a plant stoma. (c) Sporangia become detached and wind-blown, they germinate directly to form germ tubes (c_2) or produce zoospores (c_1). (d_1, d_2) Germination of encysted zoospores or of sporangia completes the asexual cycle. (e) Sexual reproduction involves the production of oogonia (♀) and antheridia (♂); in *P. infestans* the oogonial hypha grows through the antheridium but in some other *Phytophthora* species and most other oomycetes the antheridium attaches to the oogonial wall (see (e_1) inset); meiosis occurs within the sex organs, fertilization tubes (e_1) grow from the antheridium into the oogonium, and haploid nuclei pass along these to fertilize the eggs. (f) One or more thick-walled oospores (diploid) result from fertilization and persist when the sex organs disintegrate. (g)–(h) On germination the oospore produces a sporangium, and this releases zoospores (h) to reinfect a plant.

[Note that *P. infestans* requires the presence of two mating types, A_1 and A_2, for sexual reproduction (not shown in the figure), but some other *Phytophthora* spp. are self-fertile.]

Zygomycotina

Example: *Mucor hiemalis.*

Main distinguishing features of Zygomycotina

1 Vegetative state: usually a hypha, lacking septa.
2 Cell wall composed of chitosan and chitin (Chapter 2).
3 Normally haploid.
4 Asexual reproduction: by non-motile spores, formed in a sporangium, itself borne on a sporangiophore.
5 Sexual reproduction: by fusion of **gametangia** (sex organs). The resulting diploid cell develops into a spiny-walled **zygospore**, which acts as a resting stage and then undergoes meiosis to form a new vegetative generation.

Two classes: **Zygomycetes** and **Trichomycetes**.

The Class Zygomycetes includes many common saprophytic fungi, like *Mucor, Rhizopus, Mortierella, Zygorhynchus, Pilaira* and *Pilobolus* (the last two being characteristic of dung). In addition, some members of this Class parasitize insects, nematodes, amoebae or other fungi and may conceivably be used to control these organisms. Within the Zygomycetes there is a tendency to reduce the number of spores within a sporangium and, ultimately, to produce one-celled sporangia, which function as conidia (see Ascomycotina). Almost all species are terrestrial.

The Class Trichomycetes has been little investigated to date; it includes several organisms that live as commensals in the gut of arthropods in marine, freshwater or terrestrial environments.

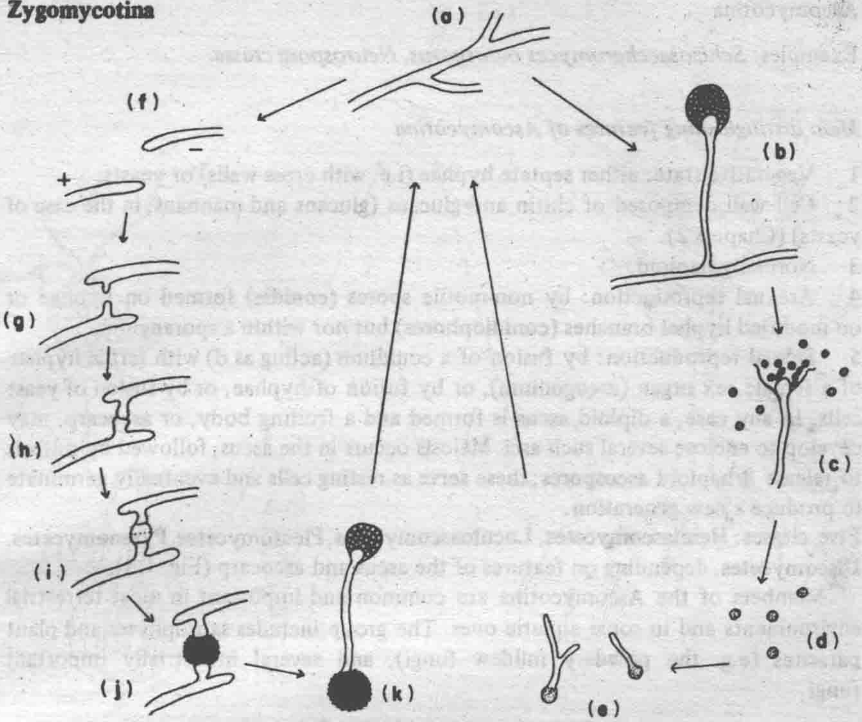

Fig. 1.5 Life cycle of *Mucor hiemalis*, a common soil saprophyte. (a) Haploid vegetative mycelium. (b) Asexual spores are borne in sporangia on aerial sporangiophores. (c)-(d)–(e) Nonmotile spores are released by breakdown of the sporangium wall and germinate to complete the asexual cycle. (f) Sexual reproduction occurs when colonies of different mating type (+ and −) are opposed; the developing sporangiophores of these colonies become modified to form sexual branches or **zygophores**, which grow towards each other under the influence of volatile sex hormones (p. 57). (g)–(h)–(i) Sex organs, or gametangia, are formed on the zygophores; these gametangia fuse and then nuclear fusion occurs to produce a diploid cell. (j) The diploid cell becomes a thick-walled resting spore, the zygospore. (k) Under suitable conditions the zygospore germinates, meiosis occurs and a sporangium is formed which releases haploid spores.

Ascomycotina

Examples: *Schizosaccharomyces octosporus, Neurospora crassa.*

Main distinguishing features of Ascomycotina

1 Vegetative state: either septate hyphae (i.e. with cross-walls) or yeasts.
2 Cell wall composed of chitin and glucans (glucans and mannans, in the case of yeasts) (Chapter 2).
3 Normally haploid.
4 Asexual reproduction: by non-motile spores (**conidia**) formed on hyphae or on modified hyphal branches (**conidiophores**) but *not* within a sporangium.
5 Sexual reproduction: by fusion of a conidium (acting as ♂) with fertile hyphae of a female sex organ (**ascogonium**), or by fusion of hyphae, or by fusion of yeast cells. In any case, a diploid **ascus** is formed and a fruiting body, or **ascocarp**, may develop to enclose several such asci. Meiosis occurs in the ascus, followed by mitosis to release 8 haploid **ascospores**; these serve as resting cells and eventually germinate to produce a new generation.

Five classes: **Hemiascomycetes, Loculoascomycetes, Plectomycetes, Pyrenomycetes, Discomycetes**, depending on features of the ascus and ascocarp (Fig. 1.8).

Members of the Ascomycotina are common and important in most terrestrial environments and in some aquatic ones. The group includes saprophytes and plant parasites (e.g. the powdery mildew fungi), and several industrially important fungi.