CHAPTER I

INTRODUCTION

THE fungi are remarkable for diversity of both form and function. Their ability to break down and to synthesize complex substances largely accounts for their success in colonizing widely different habitats, and has made them of the greatest economic importance as parasites, as saprophytes in the soil and on varied commercial products, and as the producers of antibiotics, organic acids and other substances useful to man. Even more striking is the wide range of structure and life history within the group. The vegetative part of the fungal thallus is either unicellular, as in some primitive and a few degenerate forms, or, more commonly, filamentous. These fungal filaments, which are known as hyphae, usually branch freely and together form the mycelium or vegetative thallus of the organism. In the Lower Fungi (Phycomycetes), the actively growing vegetative hyphae are aseptate and coenocytic; septa form only to cut off dead or injured parts of the hypha, or in connexion with reproduction. Such a system is not suitable for the building-up of complex structures and hence reproductive bodies in this group are usually simple. In the Higher Fungi (Ascomycetes, Basidiomycetes and Fungi Imperfecti) the hyphae are regularly septate from an early stage and, moreover, have a strong tendency to anastomose. Among these fungi, complex structures may arise through interweaving and anastomosis of the hyphae.

While the factors controlling the onset of the reproductive phase are of great intrinsic interest in all organisms, in the fungi they are also of great economic importance, since it is through their reproductive bodies that the organisms are able to spread and colonize new substrata, and often are able to survive temporarily unfavourable conditions. A knowledge of the factors inducing reproduction may thus often solve the problem of the control of parasitic and other harmful fungi. Moreover, since the classification of fungi rightly rests largely on the nature of their reproductive bodies, the physiology of reproduction is of importance also to the taxonomist.

When a reproductive unit, such as a piece of mycelium or a spore or group of spores, becomes established on a suitable substratum, as when a culture plate is inoculated, it usually produces a colony which remains in the vegetative phase for some time. Sooner or later, however, with most fungi, provided that environmental conditions are favourable, specific reproductive bodies begin to form.

TYPES OF REPRODUCTION AMONG FUNGI

(*a*) *Vegetative.* The simplest type of reproduction in fungi is the rounding-off and ultimate separation of the vegetative cells. Many fungi, such as species of *Mucor* or *Endomyces*, produce these oidia in sugary media or with increasing age. In some fungi, or under different conditions, thick-walled cells with dense contents are produced, such as the 'Dauerzellen' of the unicellular yeasts or the chlamydospores of certain filamentous moulds. These are essentially small parts of the vegetative thallus adapted to survive periods of drought, of extremes of temperature or of exposure to solutions of high osmotic pressure, which would be lethal to the ordinary thin-walled vegetative cell. Little is known of the exact factors inducing the formation of chlamydospores, but it is generally assumed that these spores are formed in response to the onset of unfavourable conditions. They are produced by relatively few fungi. The gemmae of the water moulds may sometimes be developed from vegetative cells but are commonly formed from unfertilized oogonia.

Larger vegetative reproductive bodies, known as sclerotia, are produced by a number of fungi and particularly by plant parasites inhabiting the soil. Sclerotia consist of closely interwoven hyphae, which often lose their original form so that the individual cells become globose, and are packed with reserve food substances. In some sclerotia the outer layer (or layers) of cells has become a pseudosclerenchyma with thick, often black, cell walls. Sclerotia are formed in a number of ways (Townsend and Willetts, 1954) from single hyphae or from groups of branches or hyphal strands, but their function is always that of surviving temporary food shortage, desiccation or other adverse conditions. On the return to more favourable conditions they may germinate directly by giving rise to a mass of ordinary vegetative hyphae or, as in species of *Sclerotinia* and some other genera, they may give rise to complex spore-bearing fructifications.

(*b*) *Reproduction by spores*. The most usual form of reproduction by fungi is, however, sporulation. Spores are minute separable bodies with a special form characteristic of the particular species. There are many different kinds of spore and the same fungus may produce several different types at different stages in its life history or in response to different environmental conditions.

The commonest type of spore produced by fungi is asexual: the zoospore or non-motile sporangiospore in the simpler, more primitive species, and the conidium in the Higher Fungi. These are often produced in large numbers and permit the rapid spread of the fungus under favourable conditions. While they are often slightly more tolerant than the mycelium, of adverse conditions, such as desiccation, they are not usually resistant cells as their walls are often no thicker than those of the hyphae. Asexual spores typically lack vacuoles and their cytoplasm is of a relatively concentrated nature. They are usually capable of germination as soon as they are shed but rapidly lose their viability if they do not fall on to a suitable substratum. With many fungi production of asexual spores goes on continuously or in successive waves whenever, and as long as, conditions are suitable. With many plant parasites this ceases with the approach of winter. It is not known in the majority of cases whether this inhibition is due to lower temperature or to the changed condition of the host plant itself, that is, to nutritional factors. Many fungi either do not produce any other type of spore or are not known to do so. These are included in the arbitrary group of the Fungi Imperfecti.

The majority of fungi, however, also produce a second type of spore following a nuclear fusion. In the simpler fungi, including most of the Phycomycetes, this nuclear fusion is clearly of a sexual nature and the resulting spore is a sexually produced zygote. In the Higher Fungi the fusion is not usually a clearly sexual one but takes place between two nuclei derived from mycelia of different strains or even from the same mycelium. These nuclei may pair, but fusion is often delayed. Thus spore formation does not, in many of these fungi, follow immediately after nuclear pairing but takes place after an interval during which a secondary, binucleate, phase, such as the ascogenous hyphae of the Ascomycetes or the secondary mycelium of the

Basidiomycetes, may continue for some time. Eventually nuclear fusion takes place and spore formation follows. Such spores, though they are associated with a nuclear fusion and though they are distinct from the asexual spores, cannot accurately be described as 'sexual' spores. Hence the rather unsatisfactory terms, 'perfect stage' and 'perfect spores', have been introduced to distinguish them from the asexual or 'imperfect' stage and spores.

In many Ascomycetes and Basidiomycetes the typical ascospores or basidiospores may be produced in large quantities in or on a complex fruit-body or sporophore. The hyphae forming these bodies may show considerable differentiation into layers of different function, such as the outer protective layer or periderm, a nutritive layer and the spore-bearing layer or hymenium. Some of the large perennial fruit-bodies of such fungi as *Fomes* and *Ganoderma* are exceedingly complex and of a hard woody nature.

In considering the physiology of reproduction in fungi it is obvious that the factors inducing the formation of these widely different types of reproductive body are likely to show wide differences and to be distinct from those favouring maximum production of mycelium. Further, in the development of the complex sporophores of the Higher Fungi, there is evidence that the factors inducing the initiation of these are not necessarily the same as those leading to their maturation and to the ultimate production of viable spores.

The fact that young colonies pass through a purely vegetative phase before the onset of reproduction, has already been pointed out (p. 2). The length of this initial period of vegetative growth depends partly on the environment but also largely on the age and genetic constitution of the culture. No manipulation of the environment is able to reduce this phase to less than a particular minimum value characteristic of the species or strain of fungus concerned. One must assume that reproduction does not take place until the conditions *inside* the mycelium are suitable. Such an internal condition may be influenced by the environment, but is not entirely dependent upon it. Very little is known of the nature of these internal factors inducing reproduction, but if this problem could be solved it would be a great step forward towards the understanding of the physiology of reproduction.

Even the simplest form of reproductive body is a relatively complex structure, and is certainly the result of a chain of chemical processes controlled by a large number of enzymes, all of which must either be synthesized by the fungus or acquired ready-made from the environment. Several investigators have shown (see pp. 67, 81) that reproduction in a number of fungi is preceded by a period of intense respiratory activity. It is not yet clear whether reproduction is the result of qualitative or of quantitative changes in metabolism, but in either case the process is certainly exceedingly complex. Environmental factors will thus influence reproduction if they act to modify or inhibit any stage in this long chain of events. It is not therefore surprising if apparently contradictory reports occur, since the final effect of a particular factor depends upon the particular critical stage of the reaction chain which is sensitive to it. The interplay of factors and the occasional partial replacement of one factor by another may also be better understood if it is realized that there are more processes than one involved in the metabolism of reproduction and that each process may be influenced by various factors. Some information on the mechanism by which certain nutritional and other factors may influence reproduction has been obtained by the study of artificially produced mutants of various fungi which are often more exacting in their requirements than the parent or wild type.

While the exact effect of environment must be worked out for each species or strain, and for each type of reproduction individually, it is yet possible to generalize to some extent about the factors usually favouring reproduction.

FUNCTIONS OF FUNGAL SPORES

Fungal spores have many functions. As already pointed out, the asexual spores are the main means of dispersal of certain fungi to new areas. Their simple structure and the fact that they are formed in large numbers make them an efficient means of such spread. The same function of dispersal and colonization of new substrata is also found in many of the so-called 'perfect' spores of the Higher Fungi. Ascospores and basidiospores are often produced in large numbers and may be light enough for efficient wind dispersal. Many of the Lower Fungi, however, and some of the higher ones, produce thick-walled resting spores capable of withstanding periods of drought or of extremes of temperature. Some of these spores, such as the oospores of many Oomycetes, the zygospores of the Mucorales and the teleutospores of some rusts, are incapable of germination until they have been subjected to periods of adverse conditions such as intense cold or desiccation. In those Higher Fungi in which ascospores or basidiospores are borne on, or in, complex fruit-bodies the resistance to adverse conditions depends rather on the protective layers of the fruit-body than on the structure of the spores themselves. Not only do these highly developed fruit-bodies protect the developing spores, but they are also often specially adapted for the efficient dispersal of the mature spores. It is significant that few of the higher Hymenomycetes and Gasteromycetes produce conidia to any extent, dispersal being efficiently achieved by the basidiospores.

In addition to resistance and dispersal, the 'perfect' spore stage permits the rearrangement of characters through hybridization. This is often of practical significance in agriculture, as in the well-known example of the origin, on the barberry, of new races of *Puccinia graminis* which may include forms able to attack an extended range of wheat varieties. Segregation of characters in fungi is not, however, entirely dependent on a nuclear fusion followed by a reduction division, since, owing to the strong tendency for anastomosis and consequent nuclear migration between allied strains, the nuclear content of the resulting complex mycelium is of mixed origin and may give rise to new combinations of characters (Hansen, 1938).

The significance of spores in the biology of the fungus and in man's attempts to control fungi is thus clear and the study of the physiology of the initiation and maturation of spores and spore-bearing structures is of great importance. While recent work has produced several detailed studies of spore production in particular species, the subject is one of almost unlimited opportunity.

The reproductive cycle is not complete until the spores have been discharged—often through the action of complex mechanisms—have alighted on a suitable substratum and have germinated and established a new mycelium. All these phases are influenced by the environment. They are outside the scope of the present account and have been reviewed elsewhere (Ingold, 1939, 1953; Gottlieb, 1950; Hawker, 1950; Gregory, 1952).

CHAPTER 2

THE GROWTH OF SPORES AND OF SPORE-BEARING STRUCTURES

THE physiology of sporulation in fungi can be well understood only after a consideration of the actual morphological changes involved in the growth of spores and spore-bearing structures. The whole process of reproduction, of whatever type, takes place in an orderly and more or less constant sequence of stages. It involves cell division and often coalescence of cells or adhesion of cell walls, cell enlargement, the alteration of cell shape, or of cell-wall thickness and structure, and the accumulation and differentiation of cell contents. Often the cells making up a mature reproductive body are entirely different in appearance from those of the vegetative mycelium or from those of immature reproductive structures. Those comprising a single fruit-body may be of several distinct types. Little is known of the mechanism of the actual shaping of the cells of spores and sporophores, but a few outstanding studies of the sequence of development and a few attempts to correlate visible development with the chemical and physical changes in the cell wall have been made.

SPORES

Mature spores show a wide range of size, shape, cell numbers, and pigmentation and many bear complex appendages or have elaborately sculptured walls. Spore characters are, however, remarkably uniform for any particular species. The majority of spores are colourless, single-celled, more or less globose or ovoid, thin-walled structures, and all of them pass through such a stage in the early phases of development. Fig. 1 shows the development of complex spores of various species from a single cell. We know little of the forces operating to mould the shape of spores. It is clear that if the spore is not subjected to unequal lateral pressure it is likely to remain more or less globose, provided that the spore wall develops and hardens uniformly. If, however, the developing spore is subjected to pressure from

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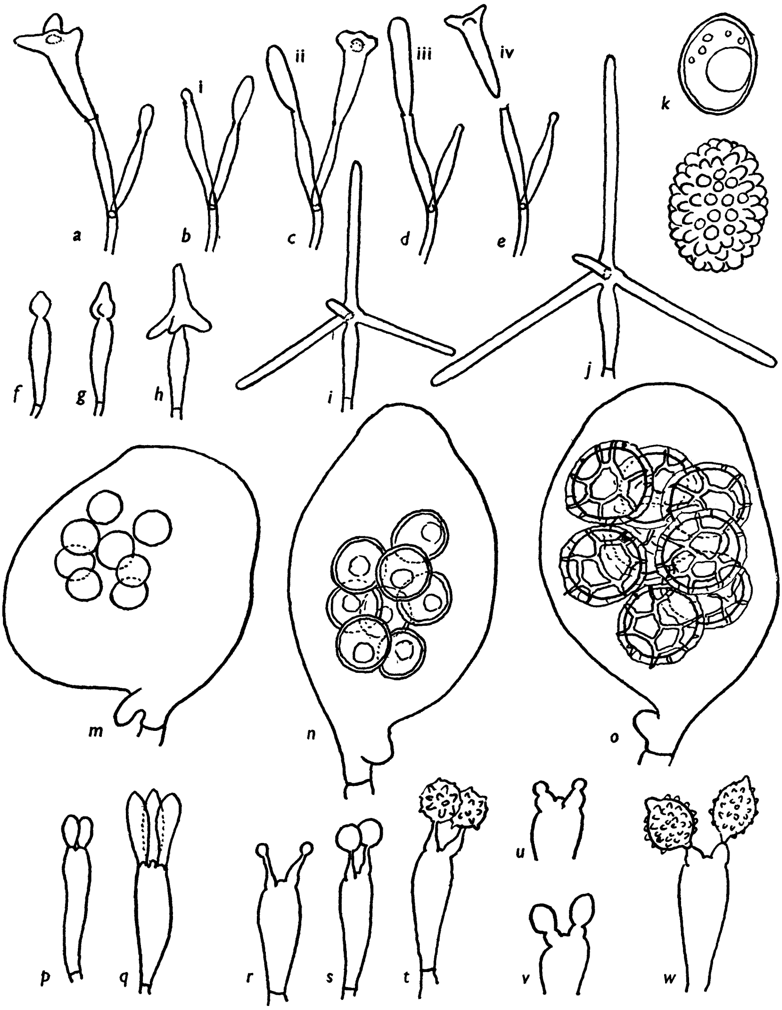

Fig. 1. Development of complex spores. *a–e*, *Heliscus aquaticus*, conidiophores with two phialides, drawn at intervals to show development of spores from each phialide alternately; i–iv show development of one such spore from small oval bud to the mature clove-shaped conidium; *f–j*, *Lemonniera aquatica*, single phialide drawn at intervals to show development of single conidium from more or less globose bud to complex four-armed spore (*a–j*, after Ingold, 1942). *k*, *l*, *Genea spherica*; *k*, immature ascospore with smooth wall; *l*, mature ascospore with hemispherical warts; *m–o*, *Hydnobolites cerebriformis*, stages in development of ascus and ascospores; *m* has immature spores with smooth thin walls; *n* has older spores, larger, with smooth thick walls; *o* has mature spores with thick, reticulately sculptured walls; *p*, *q*, *Hysterangium nephriticum*; *p*, young basidium with two young ovoid spores; *q*, mature basidium with three elongated spores with claw-like bases (number of spores on the basidium varies in this species); *r–t*, *Hydnangium carneum* var. *xanthosporum*; *r*, young basidium with small, smooth-walled, spherical spores; *s*, older basidium, spores still smooth-walled but larger; *t*, mature basidium, spores with spiny outgrowths from wall; *u–w*, *Hymenogaster tener*; *u*, apex of young basidium with small, smooth-walled spherical spores; *v*, older basidium, spores larger, ovoid, but still thin-walled; *w*, mature basidium, spores citriform, covered with blunt warts except at apex and base (*k–w*, after Hawker, 1954). ×375.

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surrounding cells and if the wall again develops uniformly it is likely, on hardening, to conform to the shape of the available space between neighbouring units. Again, if part of the wall hardens and solidifies while cytoplasm is still flowing in from the supporting hypha, the parts which are last to harden are likely to expand, as when a plastic balloon is blown up while protruding from a solid constriction. The final shape of such a spore will depend upon the location of those parts of the wall which harden at different stages in spore development. The pattern of the deposition of wall-forming molecules is obviously of importance. Cylindrical spores may be formed as a result of continuous elongation after secondary deposition of wall material begins, if the elements are laid down in such a way that intussusception of new elements can lead to expansion in one direction only.

By measuring the length and breadth of developing basidia and basidiospores of species of *Clavaria* and other Basidiomycetes, Corner (1947) showed that these all begin as globose structures and develop in a manner characteristic of each species. He concluded that, where these remain spherical, the surface increases in area evenly by uniform intussusception of new material. Where expansion continues at the apex it may be concluded that the polar cap remains elastic after the rest of the cell wall has become rigid. When the spore becomes cylindrical, the rate of advancing fixation of the wall towards the apex must balance that of enlargement of the apex, so that the latter never attains a diameter greater than that of the rest of the cell. If, however, the rate of fixation of the wall is more rapid than that of apical enlargement, a cell tapering towards the apex results, while conversely the cell tapers to the base. It has been further suggested that rigidity of the wall is due to chitinization of the original hemicellulose or cellulose structure.

When a developing cell is subjected to unequal pressure typical shapes are assumed. Thus among Ascomycetes, forms with globose asci tend to have globose, or nearly globose, spores, as with some yeasts, with certain members of the Plectascales, such as *Elaphomyces* spp., or with species of *Tuber*. Forms with clavate asci often have elongated spores (e.g. *Claviceps* and *Geoglossum*), while in the cylindrical, close-packed asci of the Pezizales, in which the spores are usually arranged uniseriately, the latter are commonly ellipsoidal and arranged at an angle to the long axis of the ascus, thus occupying the available space economically. There are, of course, many exceptions, such as the 'hat'-shaped spores of species of *Endomyces* and related genera, and the peculiar spores of many species of *Eurotium*. Both *Endomyces* and *Eurotium* have globose asci, and here one must suppose that a differential rate in wall fixation also plays a part as suggested by Corner (*loc. cit.*) for the Basidiomycetes. Ingold (1954) commented on the frequent occurrence of ascospores with a blunt apical end and a tapering base and suggested a possible biological advantage of this shape in facilitating discharge from the ascus.

Among the Hymenomycetes and Gasteromycetes, where the hymenium is extensive, the basidiospores are often more or less elongated with the long axis parallel to, or at a slight angle from, the axis of the basidium, i.e. at right angles to the plane of the hymenium. Here again one may suppose that the pressure of surrounding spores, which are often very numerous, has a formative effect. It may be remarked that, among hypogeous Gasteromycetes, those forms which shed their spores into relatively large cavities at maturity, e.g. *Hydnangium*, *Arcangeliella*, *Stephanospora*, have more or less spherical spores, while those which, like *Hymenogaster* and *Hysterangium*, retain the spores still attached to the basidia by the sterigmata for some time after maturity, tend to produce elongated spindle-shaped spores (see fig. 1).

The development of pigment and wall-sculpturing in spores must depend upon the accumulation of food materials within the spore, or on the availability of reserves in the matrix surrounding the spore, as with the cell sap of sporangia or asci. In *Bulgaria inquinans* when the nuclear division within the ascus is not simultaneous, the spores developing first may be pigmented, those developing later may be colourless, but still viable, or may abort. This is almost certainly due to competition for the available foodstuffs within the ascus. Similarly, it has been pointed out (Hawker, 1954, 1955) that nuclear divisions in the asci of truffles (*Tuber* spp.) are almost certainly not simultaneous, with the result that some of the nuclei abort; the asci thus contain irregular numbers of spores. Abortive spores of these fungi may be seen in young asci and the degree of sculpturing of the walls of the mature spores of some species may vary within the