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Excerpt
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CHAPTER I

INTRODUCTION

The Fungi are parasitic or saprophytic Thallophyta entirely destitute of chlorophyll, and possessing in the very large majority of cases a vegetative portion, the **mycelium**, made up of filaments or **hyphae**. The group is a very ancient one, the earliest known undoubted fungi occurring among the remains of *Rhynia* and *Hornia* in the Old Red Sandstone of the Muir of Rhynie, Aberdeenshire. This material consists of aseptate hyphae and vesicles which doubtless served the purpose of reproduction (frontispiece)[1].

Fungal hyphae may be non-septate and coenocytic, or they may undergo transverse septation, in which case their constituent cells are either uninucleate or multinucleate. Any division other than transverse is extremely rare; it occurs, for example, in the development of certain multicellular (muriform) spores (fig. 1), and in the initiation of the perithecium in *Strickeria* and of the pycnidium in *Pleospora* and *Phoma*[2].

As a rule the hyphae are richly branched; they elongate by apical growth and usually spread loosely through the substratum; in certain cases, especially in relation to the fructifications of the higher forms, they become woven into a dense mass which gives in section the appearance of a tissue, and is therefore described as **pseudoparenchymatous**; when fructifications are embedded in such a mass it is termed a **stroma**; a similar weft of hyphae sometimes give rise to root-like strands of which the best example is the so-called **rhizomorph** of *Armillaria mellea*, or to a compact resting body or **sclerotium** the outer cells of which are modified to form a thick-walled rind, protecting the vegetative mycelium against desiccation.

Frequent anastomoses take place between hyphae, either by means of short branches forming loops, bridges or **H-pieces**, or by means of so-called **clamp-connections** which join adjacent cells; such arrangements facilitate the passage of food and may, in certain cases, become sufficiently numerous to form a net-work.

The mycelium begins its development as a **germ-tube** put out from one of the numerous types of fungal **spore**. Where the spore wall is very thin the wall of the germ-tube may be continuous with it (zoospores), but in the majority of cases the wall of the germ-tube is continuous only with the

[1] Kidston, R. and Lang, W. H. On Old Red Sandstone Plants showing Structure from the Rhynie Chert Bed, Aberdeenshire, *Trans. Roy. Soc. Ed.* 1921.

[2] Kempton, F. E. Origin and Development of the Pycnidium, *Bot. Gaz.* 1919, lxviii, p. 233.

inner layer of the spore wall. In such cases one or more germ-tubes may break through the wall of the spore at spots not previously recognizable, or they may find an exit through special pits or **germ-pores** formed during the development of the spore. The germ-tube elongates and receives the contents of the spore.

In cases where a mycelium is not developed the plant body consists entirely of reproductive structures (Yeast, Archimycetes).

The typical fungal protoplast consists of a mass of granular or reticulate cytoplasm, which in the older regions leaves a vacuole in the centre of the cell or filament; the nucleus, where its size has permitted of detailed investigation, has a structure quite similar to that of other plants and animals, and usually divides by mitosis, showing a well-marked spindle with centrosomes and asters. The development of the spindle is extranuclear in certain Uredinales. One or more nucleoli are commonly present and are thrown out into the cytoplasm during karyokinesis. The extrusion of chromatin bodies has been described in *Helvella crispa*.

The cell wall consists of cellulose; often a special variety known as fungus cellulose is present. The storage materials include amylo-dextrin or soluble starch, amyloid, a reserve-cellulose, both of which turn blue with iodine; oil, glycogen, and various protein substances. The protoplasm gives rise also to a number of ferments which not only enable the plant to deal with its food materials, but bring into solution the walls of the host cells, and so make possible the penetration of parasitic hyphae.

Sexual reproduction among the fungi takes place by the union of two uninucleate or multinucleate cells which may be similar in structure and behaviour, or may be differentiated as an antheridium and an oogonium. Each of these organs contains one or more distinct gametes, or else a number of gametes which do not become rounded off from one another or separated from the wall of the parent cell, but are indicated by separate nuclei lying in an undifferentiated mass of cytoplasm. To organs of the latter type the term **coenogamete** is sometimes applied in recognition of their multinucleate character; it is, however, inappropriate, since they are not gametes, but gametangia. In the vast majority of fungi free swimming gametes are not developed; the sole exceptions are found in the genus *Monoblepharis*, where uniciliate or biciliate spermatozoids are set free and swim to the female organ.

A state of affairs in which the antheridium as a whole must grow or be carried to the oogonium involves a risk that normal fusion will fail to occur, while at the same time the presence of multinucleate sexual organs and of vegetative cells between which anastomoses readily occur offers considerable opportunities for some form of "reduced" fertilization. The replacement of normal fertilization by the fusion of two female or two vegetative nuclei, or of a female and a vegetative nucleus, is very common among fungi, and a complete disappearance of even this reminiscence of a sexual process is by no means rare. It has been suggested that the variety of food material which fungi as parasites and saprophytes obtain from their substratum may make the stimulus of fertilization less important, and it is possible also that among these plants competition is less severe than among holophyta or holozoa. At any rate the group shows a progressive disappearance of normal sexuality.

The sexual fusion or its equivalent is followed in all investigated cases by a reducing division or meiotic phase, so that, as in other plants or animals, the number of chromosomes is doubled in fertilization and subsequently halved in meiosis, and diploid[1] and haploid phases follow one another.

The meiotic phase is usually associated with spore-formation which, in many of the lower fungi, takes place on the germination of the zygote. In a much greater number of cases a period of vegetative development intervenes between the association of the nuclei in fertilization or otherwise and chromosome reduction, and we have a well-marked alternation of generations in which a haploid gametophyte bears the sexual cells or their equivalent, and a diploid sporophyte gives rise to spores which in turn constitute the first stage of a new gametophytic generation. It is not at all uncommon to find several sporophytes arising from a single gametophyte, and the gametophytic mycelium frequently sends out branches which grow around and protect the sexual cells and their products. Where fertilization or any equivalent process has wholly disappeared we may expect to find a similar morphological alternation of generations, though without the corresponding cytological changes; but in some cases, as in the large group of *Fungi imperfecti*, a sporophyte is no longer developed, or at any rate has not been identified.

Spores and **Spore mother-cells.** In the higher fungi the characteristic spores of the sporophyte, with the development of which meiosis is definitely associated, may be produced either *endogenously* as **ascopores** in a mother-cell of definitely restricted size termed an **ascus**, or *exogenously* as **basidio-spores** on the exterior of a cell or row of cells known as a **basidium**. The asci or basidia are frequently arranged in parallel series forming a fertile layer or **hymenium** sometimes of considerable extent. They arise from a **sub-hymenial** layer immediately below the hymenium, and among them are interpolated elongated vegetative cells or **paraphyses**, which are probably concerned in their nutrition and perhaps assist spore dispersal by keeping the mother-cells separate. The ascus and basidium and their products have long been recognized as essential features in classification.

[1] The diploid unit may be defined as a protoplast the nuclear content of which includes the double number of chromosomes.

In the lower fungi, spore formation may be associated with the meiotic phase, but the spores produced resemble those concerned in the accessory methods of reproduction.

Accessory spores. The **accessory** or non-sexual methods of reproduction have no relation to any sexual process either normal or reduced, and therefore no significance in the alternation of generations; they are devices for rapid multiplication comparable with the gemmae in *Marchantia* or the arrangements for vegetative propagation in higher plants. The spores concerned may be borne either on the sporophyte (rusts, etc.) or, as in the majority of cases, on the gametophyte.

In many of the lower fungi **zoospores** are developed in spherical, ovoid or tubular **zoosporangia**; this is the case especially in aquatic forms. In relation to the change from aquatic to subaerial conditions the contents of the sporangium may come to be shed as **walled non-motile spores**, or the sporangium may itself be set free without division of its contents. Such a structure, borne externally on its parent hypha, is termed a **conidium**, and is the characteristic accessory reproductive unit of the fungi. In the large majority of cases the conidium germinates by means of a germ-tube, but where the fungus has not completely abandoned its aquatic habit the conidium, if it falls in wet conditions, may give rise to zoospores either internally or in a vesicle borne on a short hypha. The conidia are developed either singly or in groups on **conidiophores**; these may be free, they may be gathered into a sheaf or **coremium**, or they may be formed inside a special flask-shaped receptacle known as a **pycnidium**; they show an almost endless variety in form and arrangement.

A less common reproductive cell is the **chlamydospore**; these are borne either singly or in chains in the course of the ordinary vegetative hyphae or at the ends of special branches; they are characterized, as their name implies, by an exceptionally thick wall.

In certain species and under certain conditions whole hyphae may break up into series of separate cylindrical cells or spores. Such a spore is termed an **oidium.** Oidium-formation appears to be a rapid and efficient method of multiplication and is the only one found in the fungi of such diseases as favus (*Achorion Schoenleinii*), pityriasis versicolor (*Microsporon furfur*) and thrush (*Monilia albicans*).

In these cases attempts to cultivate any more characteristic fructification have failed, and the fungus cannot therefore be assigned to any particular group.

Morphology of the spore. The individual spore whether belonging to the principal or accessory fructification is, when first formed, a **hyaline**, colourless cell; in the course of development it may divide to produce a row or a mass of cells and in the latter case is described as **muriform**;

it may also become variously coloured. In the large majority of cases the spore is enclosed by a double wall consisting of a delicate endospore and an epispore which may be smooth or variously sculptured; it may develop small projections and is then said to be warted or **verrucose**, or it may be **reticulate**, exhibiting a number of more or less regular polygonal depressions between which anastomosing ridges are present.

Many conidia and other thin walled fungal spores possess the power, in suitable media, of **budding** or **sprouting**; giving rise, that is to say, to new cells as simple lateral outgrowths which are soon nipped off. This method of propagation is shown in the conidia of the yeasts, in some of which it has wholly superseded the development of a mycelium. Ascospores are found to bud in the Exoascaceae, and basidiospores in the Ustilaginales.

Classification. The fungi are divided into three great groups according to the septation of their mycelium, and the characters of their principal spores.

FUNGI

- vegetative mycelium aseptate
  - PHYCOMYCETES
- vegetative mycelium septate
  - characteristic spores endogenous, ascospores
    - ASCOMYCETES
  - characteristic spores exogenous, basidiospores
    - BASIDIOMYCETES

They may be further subdivided as follows:

PHYCOMYCETES

- mycelium rudimentary or obsolete
  - *Archimycetes*
- mycelium well developed
  - sexual reproduction by oospores; asexual spores often motile
    - *Oomycetes*
      1. Saprolegniales
      2. Peronosporales
  - sexual reproduction by zygospores; asexual spores non-motile
    - *Zygomycetes*
      1. Mucorales
      2. Entomophthorales

ASCOMYCETES

- ascocarp, if present, either with no definite ostiole, or shield-shaped, or with asci irregularly arranged
  - *Plectomycetes*
    1. Plectascales
    2. Erysiphales
    3. Exoascales
- ascocarp wide open when ripe; asci in parallel rows
  - *Discomycetes*
    1. Pezizales
    2. Helvellales
    3. Phacidiales
    4. Hysteriales
    5. Tuberales
- ascocarp flask-shaped; opening by an ostiole when ripe; asci in parallel rows
  - *Pyrenomycetes*
    1. Hypocreales
    2. Dothideales
    3. Sphaeriales
    4. Laboulbeniales

BASIDIOMYCETES

- number of basidiospores indefinite
  - *Hemibasidiomycetes*
    1. Ustilaginales
- number of basidiospores definite, usually four
  - basidium septate
    - *Protobasidiomycetes*
      1. Uredinales
      2. Auriculariales
      3. Tremellales
  - basidium continuous
    - *Autobasidiomycetes*
      1. Hymenomycetes
      2. Gasteromycetes

SAPROPHYTISM, PARASITISM AND SYMBIOSIS

Since fungi under no circumstances possess chlorophyll, they are necessarily dependent for their food supply upon some sort of relation with another organism. As **saprophytes** they may utilize organic storage materials (sugar, etc.) or waste products, or may break up dead tissues as a source of supply; as **parasites** they may prey upon living cells with consequences to the host that vary from trifling inconvenience to complete destruction, or as **symbionts** they may establish a relationship with another organism in which the advantages are not wholly on one side.

These various arrangements are connected by intermediate forms, and by forms capable of parasitism or saprophytism according to circumstances. A species which is strictly limited to one type of nutrition is an **obligate** saprophyte, parasite, or symbiont, a species which is usually saprophytic but capable of parasitic existence on occasion, is described as a **hemi-saprophyte** or **facultative** parasite, and a form which is usually parasitic, but sometimes saprophytic as a **hemi-parasite**, or **facultative** saprophyte.

SAPROPHYTISM

According to our present knowledge the large majority of fungi are saprophytic; a considerable proportion of forms in each of the great groups and especially a very large number of the Basidiomycetes obtain their nutrition in this way.

On Wood. Ascomycetes and Basidiomycetes are important agents in the breaking up of wood; their hyphae absorb the starch and protoplasm of the unaltered cells of the wood and medullary rays and penetrate into the fibres, vessels and tracheids, either passing through the pits and especially the bordered pits, or penetrating the walls. They act upon the walls so that these become delignified and give characteristic cellulose reactions and the middle lamella is dissolved. The enzyme responsible for this change was first isolated by Czapek in the case of *Merulius lacrymans*, the fungus of dry rot. Its action seems to spread in a plane parallel to the surface of the wall either from the pits, which thus become much enlarged, or from the delicate passages left by the protoplasmic connections which originally traversed the walls of the young wood elements. The whole mass of wood loses weight and may reach the easily broken and almost powdery condition known as touch-wood. In this way considerable damage may be done to timbers (dry rot, *Merulius lacrymans*), paving blocks (*Lentinus lepideus*), etc., but also considerable advantage may ensue from the restoration to the soil of the material of fallen tree trunks, twigs and branches.

The part played by the higher fungi is here specially important as almost the only other agents of destruction of lignified tissues seem to be certain molluscs and crustacea which act by boring into the wood.

On Soil. Yeasts and filamentous fungi are abundant in woodland soils and they are also of frequent occurrence in cultivated soil; the microscopic forms show a remarkable similarity in different localities; even in Europe and America the same genera and often the same species are obtained; in culture there is a regular succession of forms, first the Mucoraceae, then *Penicillium* and *Eurotium* and later the black and brown Hyphomycetes. A large number of Basidiomycetes also develop in the soil.

The fungi of the soil utilize the sugar, starch, pectose and hemi-cellulose which are returned to the ground in dead plants and plant organs, and, in common with certain bacteria, they act upon cellulose, breaking it up into soluble substances and humus. In several cases evidence has been brought forward that some of these fungi are capable of assimilating free nitrogen but negative results have also been very common.

The activity of these fungi is well exemplified by the "fairy-rings" of dark green grass often seen in poor pastures. The soil just outside the ring is rich in the mycelium of one or two common fungi; few hyphae are found

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under the ring itself and none in the area enclosed by it. The ring is dependent upon the growth of the fungus which spreads outwards in all directions from the centre, the mycelium dying off as the food materials in the soil are exhausted; in the transition region, where the fungal hyphae themselves are disintegrating, the soil is in high condition, it contains organic residues recently formed and capable of rapid change and the grass is especially luxuriant; the ring accordingly is just inside the region of maximum fungal activity.

A certain number of fungi belonging to the Tuberales, Elaphomycetaceae, Terfeziaceae and Hymenogasteraceae are completely subterranean or **hypogeal** in their development. They produce closed fructifications protected by a stout wall of interwoven hyphae. As the spores approach maturity the fructifications develop a strong scent, varying much in character and from the human standpoint either pleasant or disagreeable, which serves to attract animals and especially rodents. The fructification is eaten and the spores pass uninjured through the alimentary canal, and are thus distributed. The truffles (*Tuber spp.*) are the best known of these forms.

Coprophilous Fungi. Fungi feeding on organic remains in the soil often benefit by the presence of natural manures and incidentally help to break up these substances so that they become available for the higher plants.

From such fungi it is no great transition to the extensive **coprophilous** flora of which the habitat is the dung of various animals and especially of herbivorous species. In addition to the rich nitrogenous food supply which these fungi obtain, the presence of cellulose in the straw and other vegetable debris in the dung is an important factor in their nutrition. This is well shown by the fact that many coprophilous species fail to fruit in artificial culture of dung decoction and agar, unless they are provided with cellulose. Cotton wool or pieces of filter paper laid on the substratum admirably serve this purpose; the latter are soon broken into small flocculent scraps. In nature Zygomycetes, Ascomycetes and Basidiomycetes succeed each other in fairly regular order and, speaking generally, show very similar adaptations to their habitat. In many Ascomycetes (Ascobolaceae, Sordariaceae) the spores are surrounded by mucilage and form together a projectile which owing to its weight can be shot to a much greater distance than would be possible for single spores. The sudden ejection of the spore mass seems to depend on the absorption of water by the mucilaginous contents of the ascus. After ejection the mass dries up and becomes firmly attached to the substratum on which it has fallen. In the same way the spores in the sporangium of *Pilobolus* are surrounded by a gelatinous envelope which swells in the presence of water and bursts the sporangium wall, so that the whole sporangium is shot off as a single mass and adheres by means of the gelatinous layer to the body against which it strikes.

The grass surrounding the dung receives an ample supply of spores and spore masses; later, if it is eaten by some herbivorous animal, the spores pass uninjured through the alimentary canal and germinate while still in the intestine or on being ejected with the dung. In some cases the wall of the spore seems to have become so effectually adapted to resist injury during its passage through the animal that it is incapable of either stretching or cracking as a preliminary to germination except after digestion or some other special treatment.

Thus de Bary succeeded in germinating spores of species *Pilobolus* and *Mucor* in water and those of *Sordaria* and *Coprinus* in nutrient solution, by exposing them to a temperature between 35° and 40° C.; Massee and Salmon obtained germination in the spores of *Ascobolus perplexans*, and *A. glaber*, after about 20 hours in either tap water or dung decoction, at a temperature of about 27° C.; I found that spores of *Lachnea stercorea* germinated in an alkaline medium (preferably dung decoction) after incubation for several hours at 38° C. (the temperature of the body of the cow), and Welsford succeeded by the same means in germinating the spores of *Ascobolus furfuraceus*, and Cutting those of *Ascophanus carneus*. Ramlow, however, describes the germination of spores of the last named species at room temperature in twenty-four hours. Further, Dodge was able to germinate the spores of several Ascobolaceae on dung agar by exposing them for 5 or 10 minutes to a temperature of 50° to 70° C., and Ramlow germinated those of *Ascobolus immersus* by sowing them on agar which was still hot after sterilization. In certain cases the action of direct sunlight was found by Dodge sufficient to induce a moderate percentage of germinations and to raise the temperature of the liquid containing the spores to about 50° C. in half an hour.

Finally, as I am informed by Mr Ramsbottom, germination may be induced mechanically by cracking or breaking the epispore, for example by rubbing the spores between two coverslips, so that all the above methods are a mere variety of means towards this end.

In the case of *Lachnea stercorea*, spores incubated for 18 to 40 hours, either in a succession of digestive fluids, or in dung extract, only germinated approximately 50 hours after the beginning of the experiment. It is probable that they do so in nature about two days after being swallowed. In *Ascophanus carneus*, also common on cow dung, germination is much more rapid, taking place under similar circumstances in a single night, so that the spores under natural conditions may be inferred to germinate while actually in the intestine. Further development, however, is in all cases dependent upon the fungus reaching the exterior of the mass of dung.

In *Coprinus sterquilinus*, Baden found that not only warmth and an alkaline medium (aqueous extract of horse dung), but the presence of certain bacteria also was necessary for germination. Appropriate bacteria may sometimes be a factor in the development of the ascocarp (Molliard) and there are many indications that certain fungi grow better in impure than in pure cultures. This, however, may merely indicate that in a mixed culture the waste products of one organism are used up by the others, whereas in a pure culture they tend to accumulate and inhibit growth. Thus Dodge found that spores of *Ascobolus Winteri* failed to germinate on the agar in which the parent ascocarps were growing.

In the case of *Mucor* and *Rhizopus*, Baden found that the presence of bacteria prevented the germination of the spores. It may be worth considering whether the progressive development of bacteria in the dung may be a factor in the succession of fungi which appear on it.

Another factor of some importance in the development of coprophilous and perhaps of other fungi is the action of direct sunlight. Cultures which remain sterile in a darkened room can often be induced to fruit by placing them in a sunny window; reference has already been made to the occasional action of sunlight on spores. Many coprophilous fungi are moreover positively heliotropic; this is well shown by the sporangiophores of *Pilobolus* and the perithecia of *Sordaria* and its allies. The ejection of the spores into an open space is in this way ensured.

Fungi on Fatty Substrata. It is probable that all or most fungi are able to utilize fats and oils; such substances are a common form of food reserve in the spores (zoospores, oospores, uredospores, etc.), in the mycelium, and especially in the sclerotia where, in the case of *Claviceps purpurea*, the proportion of fat reaches as much as 35 per cent.; in several cases the fat-splitting enzyme, lipase, has been extracted.

It is therefore not surprising that many fungi grow readily on a fatty substratum, some, such as *Empusa* and species of *Cordyceps*, on animal remains, some on other fungi and some on oil-containing fruits and seeds and on cotton, rape and other oil-cakes which are made from the waste remaining after such seeds have been crushed; they may reduce the oil content of the cake from over 10 per cent. to between 1 and 2 per cent. in two years. *Eurotium* and *Penicillium* occur on the layer of sweet oil placed over bottled fruits to prevent decomposition and together with other genera are concerned in the "ripening" of cheese. The related *Monascus heterosporus* does considerable damage in parts of Australia and New Zealand if it is allowed to get a footing on stored tallow.

Fungi producing alcoholic Fermentation. A number of fungi obtain nutriment from solutions consisting largely of soluble carbohydrates and they may also obtain energy by directly breaking up certain of these substances without the intervention of oxygen and with the formation of ethyl alcohol, carbon dioxide and small quantities of other substances. This reaction is due to the presence of the enzyme zymase and is known as alcoholic fermentation.