INTRODUCTION

The Fungi are saprophytic or parasitic members of the Thallo-phyta, entirely devoid of chlorophyll, reproduced by spores which may be sexual in origin, and possessing in most species a thallus made up of filaments, or **hyphae**,[1] which are usually colourless and together constitute the **mycelium**. The origin of the group is remote, the earliest undoubted fungi being found in the Old Red Sandstone; they consist (frontispiece[2]) of septate hyphae and of vesicles which were probably reproductive in character.

Fungal hyphae may be aseptate and coenocytic, or they may be divided by transverse septa into uninucleate, binucleate or multi-nucleate segments; longitudinal or oblique septation[3] is rare. The hyphae are for the most part richly branched. They elongate by apical growth[4] and, during vegetative development, spread loosely on and through the substratum. When fruit bodies are forming in the higher fungi, the hyphae often become woven into dense masses, resembling tissues; such masses are described as **pseudoparen-chymatous**. When the mass contains more than one fructification it is termed a **stroma**. The hyphae may also aggregate to form a root-like strand, the **rhizomorph**, or a compact resting body, the **sclerotium**; in either of these, the outer hyphae are modified to form a rind, protecting the inner regions from desiccation.

In most of the Archimycetes, and in the yeasts, where a mycelium is not developed, the vegetative thallus is converted directly into a reproductive structure, without much change in its general form.

A mycelium begins its development as a germ tube put out from one of the numerous varieties of fungal spore (fig. 1). When the spore wall is very thin, as in germinating zoospores, the wall of the germ tube is continuous with it; more often the wall of the germ tube is continuous only with the inner layer of the spore wall. One or more germ tubes may push through the wall of the spore at points not previously recognisable, or they may find exit through special pits, the germ pores. As the germ tube elongates, the con-tents of the spore pass into it. Growth and branching follow, and

[1] Clarendon (thick type) is used to indicate terms specially or mainly applicable to fungi, and which it is therefore necessary to define.
[2] Kidston and Lang, 1921.   [3] Nichols, 1896; Kempton, 1919.
[4] de Bary, 1887; Smith, J. H., 1923.

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reproductive organs may develop from some or all of the mycelial branches.

In many multicellular fungi, and occasionally in non-cellular forms, anastomoses take place between adjacent hyphae by means
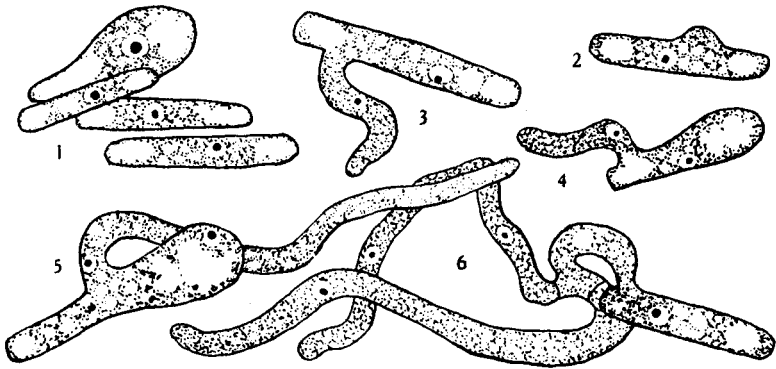

Fig. 1. *Ceratostomella fimbriata* (Ell. & Hals.) Elliott; 1, group of conidia; 2–6, stages in germination, × 1600.

of loops or branches, which, when short and straight, are known as **H-pieces**. These may connect not only branches of the same origin, but also unrelated germ tubes or older filaments (figs. 2, 3); sclerotia or fructifications grown under natural conditions, where several spores have germinated in close proximity, may accordingly be compound structures and the product of two or more spores. Such fusions are presumably nutritive in origin, and result in the pooling of the resources of several spores. Cells of the same hypha are sometimes brought into communication by means of anastomosing branches. The **clamp connections** (figs. 4, 228), common among Autobasidiomycetes, appear to fulfil a special function;[1] whatever nutritive significance they possess is limited by the fact that the passage is soon closed.[2]

Fig. 2. *Lachnea* sp.; six conidia, the germ tubes of which have undergone fusion, × 720.

Nucleus. The fungal protoplast consists of granular or reticulate cytoplasm, which, in the older regions, leaves a vacuole in the
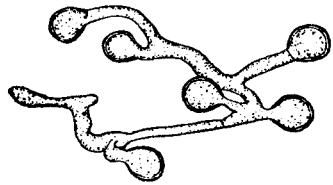
[1] Noble, 1937.   [2] Hoffmann, W., 1856; Brefeld, 1877; and cf. p. 289.

middle of the cell or filament. The nucleus may show a delicate reticulum and one or more nucleoli, or its contents may be concentrated in a dense **chromatin body** surrounded by a clear area. It usually divides by mitosis, showing a well-marked spindle with centrosomes and asters; the origin of the spindle is commonly
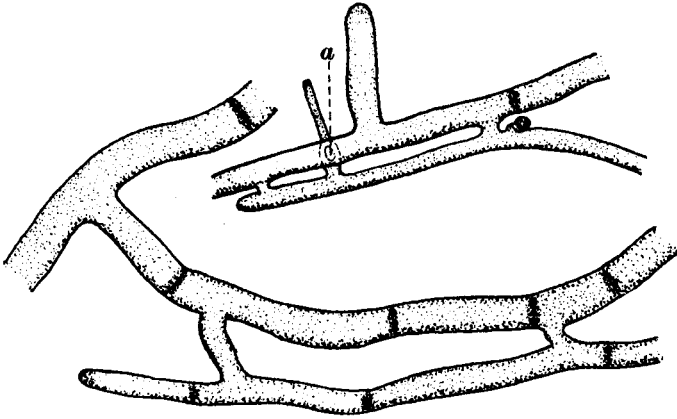

Fig. 3. *Lachnea abundans* Karst.; anastomoses between vegetative hyphae; *a*, hypha growing beneath another with a pore connecting the two, × 500.
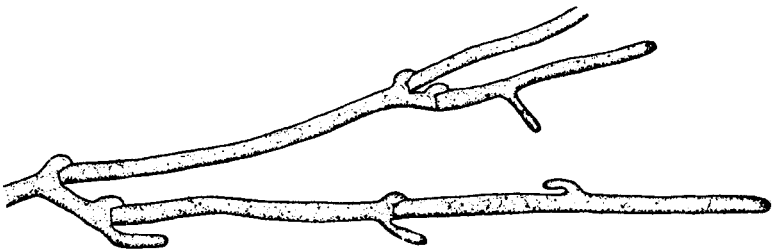

Fig. 4. *Coprinus* sp.; hyphae with clamp connections, × 675.

intranuclear, but it is extranuclear in the rusts. During the prophases of division, chromosomes are formed from the reticulum, or, if a chromatin body is present, it gives rise to chromosomes and to one or a few nucleoli. The nucleoli are thrown into the cytoplasm during karyokinesis and there disintegrate. The extrusion of additional chromatin masses has been observed in *Synchytrium* and other fungi.

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Cell Wall. The cell wall varies in composition,[1] especially in fruit bodies. In many Archimycetes and Oomycetes, and in the yeasts, the wall consists largely of cellulose, but in the Zygomycetes and the higher fungi, cellulose is replaced by chitin and other substances of obscure character. Storage materials found in hyphae include a number of carbohydrates, particularly glycogen, which is readily transformed into sugars, as well as oils and proteins. The protoplast secretes various enzymes, which not only enable the fungus to deal with its food materials, but assist parasitic hyphae to enter and break down the tissues of the host.

New transverse septa,[2] in cells rich in protoplasm, may be formed simultaneously across the whole area; when, as often happens in the higher fungi,[3] a vacuole occupies the middle region of the cell, septa result by the deposition of an annular thickening on the inner face of the longitudinal walls and its gradual extension inwards, leaving a smaller and smaller central passage, till the hole may be finally closed by a conspicuous and deeply-staining plug. So long as the passage is open, food materials pass readily from cell to cell, and, in young hyphae, where the hole is large, vacuoles and even nuclei may squeeze through. The streaming of protoplast from cell to cell is readily observed.

If, as sometimes happens, an opening is made in a mature septum, it starts from the centre and extends outwards, in the reverse order from that of wall-formation.

Sexual Reproduction. In many of the Archimycetes and in *Allomyces* among the Oomycetes, free-swimming gametes fuse in pairs to form a zygote which usually passes through a period of inactivity before developing further. In another of the Oomycetes, *Monoblepharis*, a passive or nearly passive egg is fertilised by an active spermatozoid. Elsewhere among the fungi sexual reproduction occurs by the union of the contents of two uninucleate or multinucleate gametangia without the formation of separate gametes. To a multinucleate organ of this type the term **coenogametangium** is applied. The gametangia may be similar in behaviour and structure or may be differentiated as antheridia and oogonia. In some of

[1] Wettstein, F. von, 1921.
[2] Strasburger, 1880; Gwynne-Vaughan and Williamson, 1931.
[3] Wahrlich, 1893; Gwynne-Vaughan and Williamson, 1932; Buller, 1933.

the higher fungi the whole antheridium may be detached and carried by external agencies towards the female organ; it is then termed a **spermatium** and the receptacle in which spermatia are borne is known as a **spermogonium**.

Where fertilisation depends on the union of the contents of non-motile organs a considerable risk of failure is inevitable, while the existence of coenogametangia and of frequent anastomoses between vegetative cells makes possible its replacement by the fusion of gametangial or vegetative nuclei. Among the higher fungi such arrangements are not uncommon, and the complete disappearance of the sexual stage is also frequent.

Incompatibility. Fusion between nuclei of the same gametophytic thallus, whether in sexual or vegetative cells, provides none of the chances of variation inherent in exogamy. Dioecious fungi are rare, and, though spermatia of monoecious forms may be transported to different thalli, the power of movement of attached gametangia is very limited, so that, when endogamy is possible, it is likely to occur. It is prevented in a number of species by the condition of **self-incompatibility**. In such species the vegetative thalli are divided into two or more strains. Each strain, though it may bear gametangia, can seldom produce fructifications alone, but, when two appropriate strains meet and their nuclei become associated, the characteristic structures of the sporophyte are formed. Certain species have gone a step farther and are **self-sterile**, sexual organs being formed only when two appropriate thalli are present. Usually no morphological difference exists between such **compatible** or **complementary** strains, which are conveniently described as + and − or as A and B. An obvious interpretation of such a state of affairs is that A and B differ in sex; this is probably true in the Zygomycetes, where reproduction is by isogametangia, but, in the higher fungi, self-incompatible forms are known in which the A and B mycelia are alike monoecious, bearing both antheridia and oɛgonia. It is undesirable to speak of a difference in sex between strains bearing identical sexual organs. Rather we have here, as in certain angiospermous trees, a contrivance which prevents inbreeding in a monoecious form. Often, in these self-incompatible fungi, the sexual apparatus has partially or wholly disappeared, and the union between thalli of different complement depends on mycelial fusion.

The convenient terms **heterothallism** and **heterothallic** are used to distinguish the condition of those species which have more than one strain or form of thallus, whether the difference between the forms be sexual or otherwise. A species with one strain only is said to be **homothallic**, and is both self-compatible and self-fertile.

Meiosis. The sexual fusion or its equivalent is followed in all investigated cases by a nuclear reduction or meiotic phase, so that, as in other plants and animals, the number of chromosomes, which was doubled at the fertilisation stage, is subsequently halved in meiosis, and haploid and diploid phases follow one another. As in other organisms, meiosis is concerned with the distribution of hereditary characters, and these have now been shown, in diverse groups of fungi, to be inherited on mendelian lines.

Alternation of Generations. There is evidence that, in most of the lower fungi, meiosis takes place in the germination of the zygote, but in *Allomyces* the zygote gives rise to an independent sporophyte and an independent sporophyte is also found in the rusts, in other basidiomycetous fungi, and in the yeasts. In many of the higher fungi, however, the sporophyte is parasitic on the gametophytic mycelium and obtains nutrition through it. Often several sporophytes arise from a single gametophyte, and, in many fungi, the gametophyte sends out branches which grow around and protect the sexual organs and their products. When fertilisation or any equivalent process has wholly disappeared a morphological alternation of sporophyte and gametophyte may still be found though without the corresponding cytological changes, or, as in the *Fungi imperfecti*, a sporophyte may be developed no longer.

Spores and Spore Mother Cells. In the higher fungi, the characteristic spores of the sporophyte, with the development of which meiosis is associated, may be produced endogenously, as **ascospores**, in a mother cell termed an **ascus**, or exogenously, as **basidiospores**, 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** region immediately below the hymenium, and among them are interpolated vegetative cells, or **paraphyses**, which are perhaps concerned in their nutrition, and which assist in the dispersal of the spores by

keeping the mother cells apart. The ascus and basidium, and their products, have long been recognised as essential features in classification.

Accessory Spores. The accessory methods of multiplication have no relation to a sexual process, either normal or reduced, and have no significance in the alternation of generations. They are not homologous with the spores of the Bryophyta and Pteridophyta, but are devices for rapid increase and dissemination, comparable with the gemmae of *Marchantia* or the arrangements for vegetative propagation in the higher plants. The accessory spores may be borne on the sporophyte, as in the rusts and some Auto-basidiomycetes, or on the gametophyte, as in most of the Phycomycetes and Ascomycetes.

In many lower fungi, zoospores (fig. 5) are developed in globular or tubular zoosporangia; this is especially common in aquatic forms. Related species living freely exposed to the air may shed the contents of their sporangia as walled non-motile spores, or may set free the whole sporangium, without division of its contents. The sporangium thus becomes a **conidium**, that is, a spore borne externally on a parent hypha (fig. 6), and not enclosed in any kind of sporangium. The conidium is the characteristic unit of accessory multiplication in fungi. Most often, the conidium germinates by the protrusion of one or more germ tubes, but, if the fungus has not completely lost the power of utilising fluid water as a means of dispersal, the conidium may give rise to zoospores when it falls in a wet place. Conidia are usually developed, either singly or in groups, upon stalks known as **conidiophores**; these show an almost endless variety of form and arrangement, reaching their best development in the *Fungi imperfecti*. Conidiophores may be freely exposed to the air, or they may be produced inside a special, flask-shaped receptacle, the **pycnidium**. The term **endoconidium** is applied
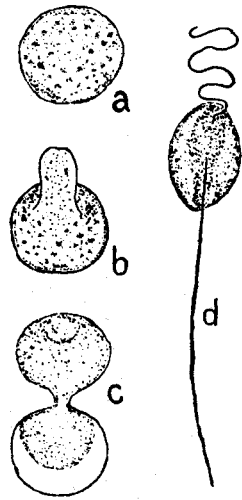

Fig. 5. *Dictyuchus* sp.; *a*, cyst; *b*, *c*, stages in emergence of the zoospore; *d*, zoospore, showing insertion of flagella; all × 1400; after Weston.

to conidia formed inside the conidiophore (fig. 7) and extruded
from it.

Resistant **chlamydospores** are formed, either singly or in
chains, in ordinary vegetative hyphae or in special branches.
Portions of the contents of the hyphae contract, lose water, and, as
the name implies, become surrounded by a thick wall.

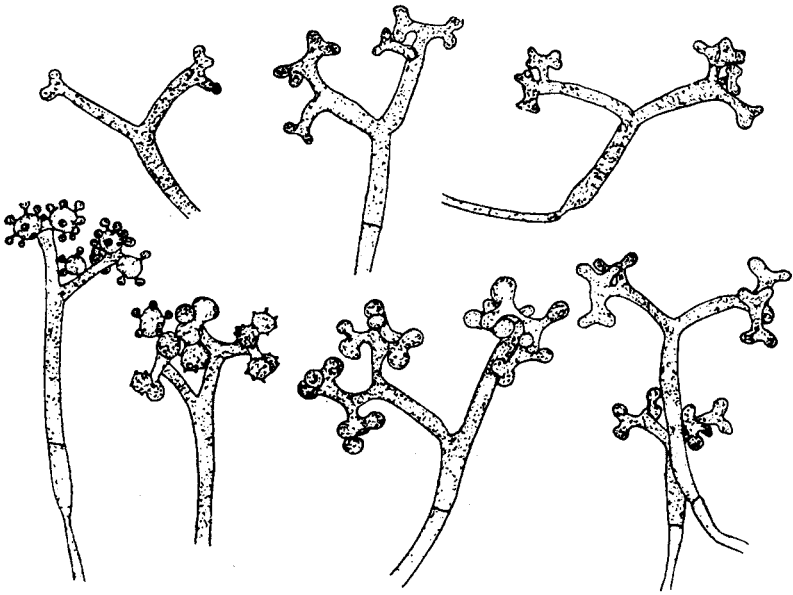In the Erysiphales and other fungi, vegetative hyphae may divide

Fig. 6. *Lachnea cretea* (Cooke) Phil.; stages in the development
of conidiophores and conidia, × 280.

into short segments, which break apart and function as asexual
spores; each such spore is an **oidium**.

Many conidia, as well as other thin-walled spores, are able to **bud**,
that is they give rise to lateral outgrowths which are nipped off as
new cells. This method of propagation occurs in the ascospores of
the Exoascaceae, and the basidiospores of the Ustilaginales. Vegeta-
tive cells may also increase by **budding**; the process is particularly
characteristic of the yeasts, many of which are unable to form a
mycelium; mycelia of *Mucor*, sunk in a fluid, may break up into

yeast-like cells, but these resume mycelial characters on transfer to a solid substratum.

Morphology of the Spore. An asexual spore, whether it belongs to the principal or accessory fructification, is, when first formed, a single, transparent, colourless cell. It may divide to form a row of cells, as does the ascospore of *Geoglossum* (fig. 75), or it may give rise to a mass of cells, then being **muri-form**, a condition found in the ascospores of *Pleospora* (fig. 76). As the spore ripens, pigments may appear in the wall or in the contents, where, too, oil globules may form. The wall of the spore is usually two-layered, consisting of a delicate endospore within an epispore which may be smooth or sculptured. In general, the sculpturing either takes the form of small isolated projections, the wall then being **verrucose**, or of anastomosing ridges separating more or less regular depressions; this is the **reticulate** condition. Spores often develop on short, special branches from the fertile hyphae, each such outgrowth being a **sterigma**.

Classification. The fungi are divided into three main classes according to the septation of the mycelium and the characters of the principal spores. The members of a fourth class, the *Fungi imperfecti*, multiply by conidia and lack a sexual process; their mycelia and conidial apparatus closely resemble those of the Ascomycetes, and it is probable that most of them are members of that class reduced or incompletely known.

The Myxomycetes are not fungi, and appear to have arisen separately from the Protista; the same is true of the Plasmodio-phorales. A summary of the salient features of these groups will be found on pp. 43–48, as well as a brief description of the *Monadineae*
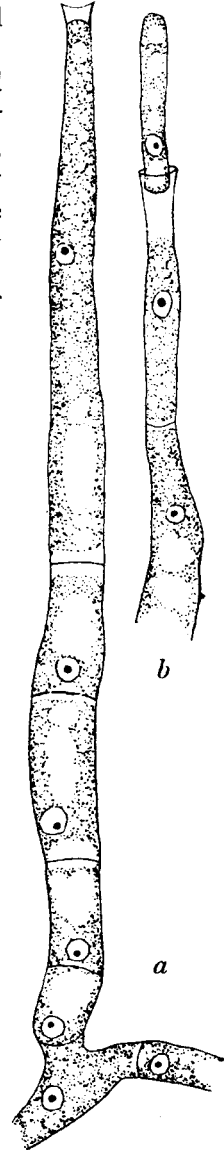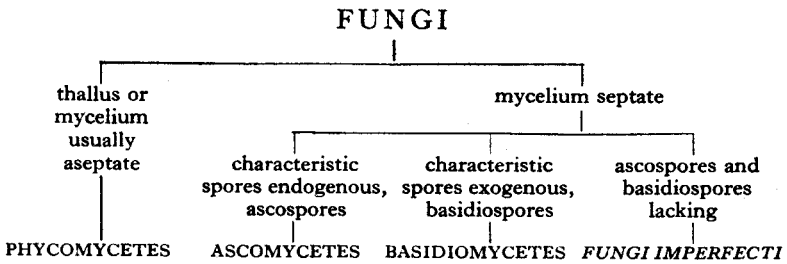

Fig. 7. *Ceratostomella fimbriata* (Ell. & Hals.) Elliott; *a*, endoconidio-phore; *b*, escaping en-doconidium, × 1600.

zoosporeae, which may represent the stock from which the Archimycetes have developed.

There are numerous works on the classification, or the classification and morphology of the fungi. Many of these are cited in the list of literature at the end of this book; among those which may specially be consulted are: Tulasne, 1861–5, of value for its admirable figures; de Bary, 1887, embodying the foundations of modern mycology; Swanton, 1909, and Ramsbottom, 1923, both useful for field work; W. G. Smith, 1908; Guilliermond, 1913; Rea, 1922; Coker, 1923; Gäumann, 1926; and the relevant portions of Rabenhorst's *Kryptogamen-Flora*, and Engler and Prantl's *Pflanzenfamilien*. The figures given in many of the above-named books may be used to supplement those in the present text.

The classes of fungi may be distinguished by the following characters:

FUNGI

thallus or mycelium usually aseptate		mycelium septate	
	characteristic spores endogenous, ascospores	characteristic spores exogenous, basidiospores	ascospores and basidiospores lacking
PHYCOMYCETES	ASCOMYCETES	BASIDIOMYCETES	*FUNGI IMPERFECTI*

They may be subdivided as follows:

PHYCOMYCETES

mycelium absent or rudimentary			
	mycelium well developed		
		sexual reproduction by oospores; accessory spores often motile	sexual reproduction by zygospores; accessory spores non-motile
ARCHIMYCETES		OOMYCETES	ZYGOMYCETES
1. Chytridiales		1. Blastocladiales	1. Mucorales
2. Ancylistales		2. Monoblepharidales	2. Entomophthorales
3. Protomycetales		3. Leptomitales	
		4. Saprolegniales	
		5. Peronosporales	