

Outline of Mycology

M.Langeron and R.Vanbreuseghem

Translated by J.Wilkinson

OUTLINE OF MYCOLOGY

M. LANGERON
(1874–1950)

Second edition revised by
R. VANBREUSEGHEM, M.D.

Translated from the French by
J. WILKINSON, Ph.D., F.L.S.
Department of Botany, University of Exeter



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Foreword

The second edition of Dr. Langeron's *Précis de Mycologie*, as enlarged and revised by his friend and former pupil, Professor R. Vanbreuseghem, was published in 1952, two years after Langeron's death. It consisted of three parts, the third of which was written by Vanbreuseghem. This was translated into English by Dr. J. Wilkinson and published in 1958 as *Mycoses of Man and Animals*, by R. Vanbreuseghem. The first part of the *Précis* is concerned with general mycology and its translation constitutes the present volume. It contains a wealth of mycological information not available in any other book which I have seen. Dr. Langeron adopted an approach based on developmental morphology, rather than the standard taxonomic treatment found in most mycological texts. Although his classification of "lower" fungi into Archimycetes and Phycornycetes and his very wide interpretation of sexuality in Fungi are not wholly in line with current thinking, the chapters on morphology and spore discharge and dispersal, which constitute the bulk of the book, are full of useful information brought together from diverse sources for the first time. Of particular interest and value are the detailed descriptions of spore development and morphology, aspects which are now being used in attempts to devise a more rational and perhaps more natural classification of Fungi Imperfecti than the system of Saccardo in present use. The liberal use of Buller's excellent illustrations is another valuable feature. Dr. Wilkinson is to be congratulated on the quality of his translation, which mycologists in English-speaking countries throughout the world will welcome and appreciate.

S. A. J. TARR, *University of Exeter*

Preface to the First French Edition

Pourquoi ce livre ? Je n'ai jamais eu de prédilection pour les champignons, mais mes Chefs hiérarchiques, les Professeurs Raphaël Blanchard, puis Emile Brumpt, son successeur, m'ont toujours vivement et amicalement conseillé l'étude de ce groupe. Le Professeur Brumpt a même créé, en 1930, dans son Institut de Parasitologie et grâce à l'aide généreuse de la Fondation Rockefeller, une section de mycologie médicale, dont il a bien voulu me confier la direction. De sorte qu'il y a eu chaque année, depuis 1929, dans cet Institut, un enseignement mycologique comportant 25 séances de démonstrations pratiques et commentées.

J'ai donc étudié les champignons et, s'ils n'ont pas ému ma sympathie, ils ont du moins forcé mon admiration. Car ce sont des êtres étranges et redoutables, spécialistes de l'arme chimique, si perfidement dissolvante. Mes anciens élèves m'ont souvent demandé de rédiger mes leçons et de composer pour eux un livre d'initiation à la mycologie générale et médicale, en expurgeant cette dernière des extravagances qui l'encombrent et l'obscurcissent. D'où ce *Précis*, que MM. Masson et Cie ont bien voulu éditer, malgré de grandes difficultés matérielles, ce dont je les remercie très vivement.

Aux lecteurs, je ne puis mieux faire que de transmettre le message de Dante—

Messo t'ho innanzi: omai per te ti ciba.

M. LANGERON

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CHAPTER I

Fungi and Protista

IN works on botany, fungi are usually regarded as plants, but this is of doubtful validity. A rigid definition of a plant, quite impossible in practice, is essential to this view, and there is no fundamental and absolute distinction between the animal and plant kingdoms. Claude Bernard long ago exploded the doctrine of vital duality.

Superficially considered, fungi exhibit certain of the more obvious features of plants. The fleshy fungi with cap and gills, such as agarics which catch the eye in meadows, heaths and the margins of woods and forests, grow upon the ground and appear to be rooted like plants. The same applies to those which grow on living or dead tree-trunks; apparently rooted in bark, they also have a cap, and except that there are tubes rather than gills beneath it, the same can be said of boleti growing in soil. Lastly, there are fungi of a somewhat bushy or shrubby habit, also apparently rooted in the earth or upon tree-stumps; such are clavarias, phylacterias (often confused with thelephoras), and certain branching polypores such as *Polyporus giganteus*, *P. frondosus*, and *P. umbellatus*. Certain filamentous fungi resemble green algae which have lost their chlorophyll, and are thus called Phycomycetes, or "algal fungi."

If, however, as Buller has done, fungi are subjected to detailed examination rather than a superficial glance; if, with the aid of simple technical procedures, microscopic examination is carried out upon the hyphae of an active young culture obtained by growing, upon a suitable medium, the spores of a cap fungus such as *Coprinus*, or those of a mould such as *Mucor* or *Rhizopus*, the results will no longer wholly support the view that one is dealing with a plant.

Tubular structures, containing more or less granular protoplasm in motion, with nuclei in suspension and vacuolar inclusions here and there, will be seen. The fungus should be examined in the living condition, upon its culture-medium, on a slide or in a hanging drop, without fixatives or staining reagents, not even vital stains.

Patient study soon shows that the cytoplasmic movement is orderly and follows a definite pattern, namely a centrifugal streaming from the centre to the periphery, such that the cytoplasm accumulates at the growing apices of the filaments in the regions of continuous growth. As a result, cytoplasm imperceptibly leaves the oldest regions of the mycelium; these regions, full of gradually enlarging vacuoles, retain a parietal layer of cytoplasm for a time, then this eventually disappears. These empty moribund portions of the filaments are usually cut off by septa from the living regions.

There are thus two correlated movements; one, an outwardly flowing stream which drives the cytoplasm towards the growing tips of the filaments, where it accumulates; and the other, a vacuolation which is also centrifugal: the vacuoles appear, enlarge, and, by exerting pressure upon the cytoplasm, push it towards the region of growth.

These cytoplasmic and vacuolar movements, as well as those of the nuclei which accompany them, will later be given detailed attention. It is noteworthy that cytoplasmic streaming may occur over considerable lengths of filament and regardless of the presence of septa, for, except for certain special cases, the septum has a small central pore which permits the ready passage of cytoplasm and nuclei. Indeed, contrary to widespread belief, all living portions of a mycelium, even though septate, are in constant communication by means of the incessantly streaming cytoplasm.

This is true even for very large fruiting bodies such as those of certain agarics and boleti. In these the cytoplasm moves continually towards its objective, the spore; from the hyphae it passes into the basidia, then these in turn become vacuolated as the cytoplasm and nuclei are driven, under heavy pressure, through the ultracapillary spaces of the sterigmata. When the last basidiospore has been shed as a result of this constant pressure, the basidiocarp dies and rapidly disintegrates.

Though this example is taken from the Basidiomycetes, the same is true of the Ascomycetes, the filamentous Phycomycetes, and the Fungi Imperfecti. The process is more or less distinctive and easy to observe in particular cases, but is none the less fundamental.

A typical hyphal fungus thus appears essentially to comprise a *nucleated cytoplasmic mass, mobilized in a system of tubes*. All that here follows concerning the cytology, anatomy and physiology of fungi turns on this, whatever the form of complexity of a thallus or a sporophore. Are these to be regarded as characteristic of plants?

Plants are traditionally regarded as immobile, of relatively low irritability, and comprising colonies of cells rather than individuals. Now fungi have characteristics which are diametrically the opposite of these; they frequently move (zoospores); they are irritable, as may easily be observed under the microscope by bringing them into contact with fine metal or glass needles, exposing them to a powerful light ray, or even better by observing the predatory fungi, of which the various trap-mechanisms are later described; their cytoplasmic continuity is considerable and constant, extending to all living parts of a thallus which may weigh several kilograms; and finally, they are not colonies of cells, but tubular individuals of integral construction, as is evidenced by study of their cytoplasmic and nuclear movements.

Are they then to be regarded as animals? Not at all, because of their great power to synthesize. There is, however, an ill-defined class of organisms in nature, with such features common to plants and animals that they have been variously placed in the one or the other group. These

are the *protista*, possessed of extremely simple anatomical and morphological characteristics, but whose physiological complexity rivals that of any other plant or animal. This group gave rise to the study of protistology initiated by Haeckel (*Generelle Morphologie*, Berlin, 1866).

According to Wenyon¹ (1926), a typical member of the protista is made up of a mass of cytoplasm and a nucleus provided with chromatin. The nucleus is delimited from the cytoplasm by a nuclear membrane. Further, the cytoplasm may possess various inclusions.

It follows from this traditional concept that protista are unicellular. There are, however, two possible views, that of Schwann (1839) and that of Dobbell² (1911).

On the classical view, the thallus of a representative of the protista is equivalent to one of the cells making up the body of an animal or higher plant, which makes the latter multicellular whilst protista are unicellular.

Dobbell, on the contrary, regards protista as non-cellular organisms, the whole individual possessing the status of multicellular organism; but whereas, in the latter, the nucleated cytoplasm is distributed among separate cells, in the protista it remains single and simple. Nevertheless, in certain instances the cytoplasm of protista may contain several nuclei.

According to Dobbell, protista are thus *non-cellular* or *acellular*, in contradistinction to other organisms which are termed cellular, and it follows that protista should be assigned to a kingdom distinct from those of plants and animals. This "Protista Kingdom" includes the protophyta and the protozoa as well as other acellular organisms of doubtful affinities. Cellular plants and animals are *metaphyta* and *metazoa* respectively.

Langeron and Guerra have, since 1938, applied this conception of protista to the levuriform (yeast) fungi, claiming that the yeast cell is a complete organism,³ a protistan, as is that of *Amoeba*, according to Dobbell's conception. We propose here to extend this view to all fungi, basing our findings upon the work of Buller on cytoplasmic streaming.

In the chapter dealing with this, it will be seen that all fungi are really *coenocytic*, that is, *acellular*. It has already been stated that septa impose no obstacle to the circulation of cytoplasm and nuclei, on account of their central pore which, though narrow, permits such circulation. Moreover, the channel within a basidial sterigma is even more greatly reduced, yet it permits the passage of nucleate cytoplasm to the basidiospore. It will further be seen that truly complete septa only occur where living and non-living regions are separated from one another.

Buller's observations were reported to be exclusively on living fungi without the use of any reagent, or even of vital staining; and direct examination of fresh material has here been abundantly justified.⁴ Besides,

¹ Wenyon, C. M., *Protozoology*, 1, 5, 152 (1926).

² Dobbell, C., The principles of protistology, *Arch. Protistenk.*, 23, 269-310 (1911). See also Franz, V., Was ist ein "höherer" Organismus?, *Biol. Zbl.*, 31, 1 (1911).

³ This is not the view of Wickerham and Retger (*J. Trop. Med. Hyg.*, 42, 174, 187, 204 (1939)), who have observed septate filaments in *Candida albicans*.

⁴ See Langeron, M., *Précis de Microscopie*, 7th ed., p. 362, (Paris, Masson, 1949).

fungi are much more difficult to fix, embed, section and stain. The most appropriate species must be chosen for this type of investigation; they must be maintained in microculture, and much time must be given to the exact observation of transient phenomena under very high magnifications. Cultures must be multiplied and examinations frequently repeated. Very good optical equipment, especially of the phase-contrast type, is necessary for observation of living material.¹

Another characteristic feature of Protista is encystment,² whether seasonal, at the beginning of winter, or simply periodic, upon exhaustion of the medium in which the organism lives.

Encystment is almost invariably the rule in free or parasitic Protozoa. Of the Protozoa parasitic in the human intestine,³ it is only in the species of *Trichomonas* that the perfect cyst stage is not known. In other species the presence of cysts in stools is an important diagnostic feature, because of their characteristic shape and size.

Encystment may take place at any stage in the life cycle of Protozoa. Often cysts are purely vegetative and simply propagate the individual, but they may also act as propagating or multiplying structures. Thus, in amoebae parasitic on man, multiplication occurs inside the cyst, where the nucleus divides to produce eight daughter nuclei in *Entamoeba coli*, and four in *E. dysenteriae*, *E. dispar*, *E. hartmanni*, etc. In Coccidia and Gregarines the zygotes encyst (oocytes) and produce a sometimes considerable number of sporozoites, with or without intermediary sporoblast or sporocyst, or secondary cyst, stages within the oocyte. Some Infusoria (*Colpoda*) may also form daughter cysts inside the mother cyst. The cyst stage occurs even in certain flagellates (*Prowazekella*). These examples of cyst polymorphism are relevant, since they permit a better interpretation of the various cyst forms in fungi.

In the latter, encystment is likewise a normal occurrence. The cyst type in fungi is the chlamydospore. In general, this spore type is neither a form of reproduction nor a propagating cell: it is a vegetative resting cyst. It will be seen that the chlamydospore arises by cytoplasmic condensation, at the expense of one or more cells of the mycelium or pseudo-mycelium, as in *Candida albicans*, a yeast-like fungus strictly characterized by the presence of chlamydospore clusters (Langeron and Guerra, 1938).

In some yeasts which rarely, if ever, form a pseudo-mycelium, such as *Torulopsis pulcherrima*,⁴ the chlamydospores are single and rather like

¹ See Langeron, M., *Précis de Microscopie*, 7th ed., p. 252 (Paris, Masson, 1949).

² Encystment is of widespread occurrence, even in groups which are relatively highly evolved. Apart from Protozoa, there are gemmules in the sponges, statoblasts (Allman, 1856) in the freshwater Bryozoa (*Cristatella*), winter eggs in the Cladocerae, cysts in the Myxobacteriales, &c.

³ See Brumpt, E., *Précis de Parasitologie*, 6th ed. (Paris, Masson, 1949).

⁴ *Torulopsis pulcherrima* (Lindner) Lodder 1934 is a yeast common on flowers and fruits. Beijerinck (*Folia microbiologica*, 1, (75 (1912)) found it on raisins, honey (especially heather honey), flower nectar (especially from labiates, e.g. *Lamium*), the crop of bumble-bees, dust from polished barley seed, etc. Lindner, author of the species (*Wsch. Brau.*, 4, 853 (1887)), isolated it from stewed plums, raisins and excrement of apple-maggots. *Torulopsis pulcherrima* has probably wrongly been introduced into medical literature and considered by various

the cysts of Protozoa. They are large cells (3.5–6 μ , while the blastospores of this yeast measure only 2.5–3 μ) rounded, thick-walled with a somewhat mucilaginous capsule and a lipid inclusion, which caused Beijerinck to¹ call them "fatty yeasts."²

The hypnospores of some groups of Phycomycetes must also be regarded as cysts, i.e. chlamydospores. These hypnospores may be zoosporangia as in Chytridiales; in the genus *Woronina* (*W. polycystis*) the hypnospores may cluster to form a large composite, verrucose chlamydospore called a cystosorus, while in some Saprolegniales the zoospores themselves encyst either inside the sporangium or after a period of freedom (cystospores).

Again, in *Aphanomyces* (Leptomitaceae) the oospore assumes the characteristics of a chlamydospore; this also occurs in Peronosporales, while in Mucorales the zygosporangium becomes thick-walled and often verrucose.

In Entomophthorales the function of a chlamydospore is carried out either by special thallospores or hyphal bodies, or by buds produced from these bodies, or by the zygosporangium, or by certain vegetative cells of the thallus (in *Completozia complens*, parasitic on fern prothalli).

Apart from cytoplasmic streaming and encystment, Protista are characterized by movement. In Protozoa there are Plasmodroma,³ which move by means of pseudopodia or flagella, in contrast to Ciliophora, where locomotion is by means of vibrating cilia. Similarly fungi may be regarded as plasmodroma-like organisms, since the cytoplasmic mass, whether free as in Myxomycetes or enclosed in hyphae as in Eumycetes, always moves in the form of pseudopodia or streams. The analogy may be pursued further, since Protozoa of the Plasmodroma have two main classes, Rhizopoda and Mastigophora, depending on whether they have flagella

authors to be a yeast pathogenic to man (*Monilia castellani* S. Re, 1925; *Torulopsis castellani* Castellani and Jacono, 1933; *Cryptococcus interditalis* Pollacci and Nannizzi, 1926). This yeast is easily recognized (see Langeron and Guerra, "Les secteurs clairs et sombres des colonies de levures," *Ann. Parasit.*, 18, 101–4, p. 1. V, Figs. 8–12 (1941)). The colonies stain red in presence of a trace of soluble iron salt and produce large chlamydospores. The deep red pigment may diffuse through the agar mass, staining it to a variable extent, or impregnate the yeast cells themselves. Beijerinck studied the origin of this colour (1918): the yeast produces a colourless chromogen which, in presence of traces of a soluble iron salt and oxygen, yield this highly coloured pigment by oxidation. This is easy to demonstrate by adding to agar 10 mg per cent of ammoniacal iron citrate or other soluble ferrous or ferric salt. But, in general, staining occurs spontaneously because of traces of iron in crude glucose.

Beijerinck's observations have been confirmed by Roberts ("The effect of iron and other factors on the production of pigment by the yeast *Torulopsis pulcherrima*," *Amer. J. Bot.*, 33, 237–44 (1946)). On the other hand Porchet (*Ann. des Ferment.*, 4, 385–405 (1938)) refutes the necessity for iron.

¹ *Arch. néerl. Physiol.*, 2, 609–15 (1918).

² Lipid formation is common in yeast-like fungi. Attempts have been made to exploit this property industrially, e.g. with *Endomycopsis vernalis* (Ludwig, 1896) Dekker and *Torulopsis lipofera* den Dooren de Jong, 1926. *E. vernalis* occurs in birch and beech sap exudates, *T. lipofera* in a soil culture from near Delft (Holland). *Torulopsis pulcherrima* and *Nectaromyces renkauffii* (A. Rippell, 1943) have also been used. See Raaf, H., *Arch. mikrobiol.*, 12, 132–82 (1941); von Soden, O. and Dirr, K., *Biochem. Z.*, 312, 263–76 (1942); Stampa, G., "Etat actuel de la synthèse biologique des matières grasses et de ses possibilités industrielles," *Rev. int. agr.*, 33, 445T and 53T (1942).

³ Some authors have divided the Protozoa into two subphyla, the Plasmodroma containing the Mastigophora, Rhizopoda and Sporozoa, and the Ciliophora, containing only the Ciliata.

or not. Flagellated and non-flagellated stages can occur together in the same species, at different points in the life cycle. The same situation prevails in many fungi (Archimycetes, Chytridiales and Oomycetes) in which the flagellated stage is represented by zoospores. Further, Plasmodium are either uni- or multinucleate, as in fungi.

These similarities suggest that there is no serious objection to uniting fungi, in the widest sense, including Myxomycetes, with Protozoa and Protophyta in the Protista.¹ The concept of three kingdoms, Protista, Metaphyta and Metazoa, is as tenable as many others, and has the great advantage of including organisms of uncertain affinities, bridging plants and animals.

The view of fungi as Protista involves certain modifications of accepted ideas on phylogeny. For example, the phylogenetic hypothesis of progressive degradation, paradoxically relating to the most highly-developed forms, which is detailed in the classic work of Gäumann,² and which presents not only an excellent comparative study of anatomy, morphology and embryology in fungi, but also data linked and clarified by cytological and genetical considerations, appears to be very plausible. However, the whole concept is based on the assumption that fungi proper (excluding Myxomycetes and Archimycetes) are derived from green algae in a monophyletic line, which is not supported by precise fact.

Sexual phenomena, which are fundamental to Gäumann's argument, are almost identical in all Protista. It is unnecessary therefore to trace the derivation of fungi from the Chlorophyceae. They could equally well have arisen from the same line as Myxomycetes and Archimycetes.

A monophyletic view of the origin of the fungi would appear reasonable, and far removed from the views of Pringheim (1856), Cohn (1874), Sachs (1874) and from the polyphyletism which connected Chytridiales with Protococcaceae, Zygomycetes with Conjugatae and so-called higher fungi (Ascomycetes and Basidiomycetes) with Florideae or red algae as if the loss of chlorophyll occurred in several algal groups, with concomitant transition to the saprophytic or parasitic habit. This theory is no longer held except by certain North American botanists (C. and E. Bessey and co-workers).

Most biologists and botanists have accepted the view of De Bary, who, in 1881, opposed the polyphyletic concept. De Bary regarded both algae and fungi as being derived from primitive organisms (in our view, Protista) with or without chlorophyll, and as having developed along parallel lines. He considered the physiological differences between an organism containing chlorophyll and one without chlorophyll to be too great for transition to have occurred several times in algae.

¹ See Pavillard, J., "Etat actuel de la protistologie," *Processus rei botanicae*, 3, (1910) 474-544; Cavers, F., "The interrelationship of Protista and primitive fungi," *New Phytologist*, 14, 94-104, 104-68, 223-7, 275-80, 302-4 (1915).

² Gäumann, E., *Vergleichende Morphologie der Pilze*, 628 pp. (Jena, Fischer, 1926). Translated into English by C. W. Dodge, *Comparative Morphology of Fungi*, 701 pp. (New York and London, McGraw-Hill, 1928).

The present trend appears to be to regard flagellates as the most primitive protistan type and as the hypothetical single source of Metaphyta and Metazoa. Among flagellates, the prototype is generally taken as the *Euglena* group, which has chlorophyll in chloroplasts. This pigment is not absolutely indispensable, for *Euglena* can survive without it under certain natural or experimental conditions. This supports the transition hypothesis whereby two series of organisms arose, with and without chlorophyll.

If the *Euglena* prototype is accepted, separation might have occurred from the first with the two lines, algae and fungi, exhibiting parallel development as De Bary proposed. If so, there is no need to assume a progressive sexual degradation compensated by progressively greater morphological complexity.

Furthermore, it is difficult in fungi to talk of "degraded" organisms; the striking fructifications of *Agaricus* or *Boletus*, the amazing mechanisms of Clathraceae (*Clathrus*, *Simblum*, *Colus*, *Anthurus*, *Aseröe*, *Calathiscus*, *Kalchbrennera*, etc.) and Phallaceae (*Ithyphallus*, *Mutinus*, *Echinophallus*, *Dictyophora*, etc.), the surprising polymorphism of all groups and their no less extraordinary metabolic activity are manifestations of great vitality. As for sexuality it will be seen that very few organisms exhibit as many different forms. It is clear that far from demonstrating great and progressive degradation, or even regressive evolution, this indicates extreme plasticity, which permits flexibility in coping with changing conditions. It is correlated with the histological and morphological complexity of these organisms and especially with their Protista-like physiology, being as they are plasmodial organisms, whose vacuolated plasmodium is either free or confined in tubes where it is subject to osmotic and capillary forces.

Also, any phylogeny not based on palaeontological fact is quite irrelevant. Now, for fungi, palaeontological evidence is almost non-existent. Meschinelli¹ in Vicenza in 1898 published in iconography of all fossil fungi known at that time. Later, Lindau prepared the chapter on fossil fungi for Engler and Prantl's *Natürliche Pflanzenfamilien*.² These remains are either impressions or true fossils preserved in silicified wood, in coal or even in amber; their identification, always very difficult, is usually controversial. This information seems insufficient as a basis for a phylogeny; only research on living fungi is likely to indicate types which may be regarded as the most primitive or as relics of a former age.

Even here there is much controversy and it is usually necessary to invent imaginary primitive or intermediate types to bridge gaps and unite existing groups. But there is no proof that these types actually existed.

Finally here is the conclusion to Dodge's paper³ to the 3rd International Congress of Microbiology (New York, 2nd-9th Sept., 1939): "I have tried to show that fungi are not degenerate organisms, which have developed

¹ Meschinelli, A., *Fungorum fossilium omnium hujusque cognitorum iconographia* (Vicenza, 1898).

² Vol. I, Part I, pp. 518-23 (1900).

³ Dodge, B. O., "Some problems in the genetics of fungi," *3rd International Congress for Microbiology*, New York, September 2nd-9th, 1939, *Rep. of Proc.*, pp. 107-18 (1940).

against the evolutionary trend. Fungi, on the contrary, are progressive, always changing, and evolve rapidly on their own lines, so that they are capable of prompt adaptation to any situation. We may be sure that while green plants and animals disappear gradually from the surface of the globe, there will always be fungi to utilize their last remains."

CHAPTER II

General and Systematic Characteristics of the Fungi

A. GENERAL CHARACTERISTICS

FUNGI are here regarded as allied to Protista, for reasons already given. It may be objected that Protista are usually microscopic organisms; this, however, really applies to fungi. Some have large fructifications, but the majority are almost invisible to the naked eye, and the fruiting body, which is usually ephemeral, is not the whole fungus.

The fungus is the thallus or mycelium, often invisible because hidden in the substratum, and typically composed of very slender microscopic filaments. The mycelium is the tubular structure containing the cytoplasmic mass which properly constitutes the fungus. This concept of fungus-protista greatly simplifies the general ideas which are dealt with here. Fungi need not be compared with other plants, since they are not plants. Within the Protista they form a separate group, distinguishable by the following characteristics.

1. VEGETATIVE STRUCTURE

This is usually a filamentous thallus (from *θαλλος*, bough, young branch) which, whatever its extent and ramification, is composed solely of filaments, called mycelial filaments or hyphae (from *υφη*, tissue). These constitute the mycelium, a name frequently given to the thallus, and are characterized by their exclusively terminal growth and by the presence of true branching. The development of the mycelium as a whole is centrifugal, leading to the production of a more or less compact network in three dimensions. There is never a true tissue in the fungal thallus, but the nuclei circulating in its filaments resemble those of higher plants.

2. HETEROTROPHISM

Fungi are completely lacking in chlorophyll and all chlorophyllous pigment. Consequently, as in bacteria, there is no true starch and they must extract carbon, not from carbon dioxide in the air but from more complex substances manufactured by other organisms. Fungi are therefore heterotrophic, in contrast with autotrophic, chlorophyll-containing organisms. Thus they are of necessity saprophytes or parasites. They can, however, extract nitrogen from mineral substances (nitrates, and especially ammonium salts).

3. GEOTROPISM

Very variable and connected mainly with spore dispersal. Purely filamentous fungi seem to be insensitive to geotropism: the mycelium develops over the supporting surface and the aerial fructifications are generally perpendicular to this. These facts are easily verified by examining colonies on agar slopes in vertical tubes.

This does not apply to fungi with sporophores; there the stipe is always negatively geotropic, but this geotropism is clearly evident only from the movement when the cap develops. Geotropism of pseudorhiza is always negative.

The geotropic reaction of the hymenium differs according to whether it produces ascospores or basidiospores: the hymenium of Ascomycetes with discoid or cup-shaped fruiting bodies (Discomycetes) is negatively geotropic and in particular phototropic, while that of Basidiomycetes, distributed upon lamellae, or in tubes or heads is positively and strongly orthogeotropic, except in inequihymenial types such as *Coprinus* where the lamellae are ageotropic (indifferent). The caps of Hymenomycetes are diageotropic.

4. PHOTOTROPISM

Strongly developed in coprophilous fungi of all kinds, whether microfungi or macrofungi. It is also very marked in the asci of Discomycetes on which the effect is more powerful than that of gravity.

Darkness can produce curious effects: for instance fructifications of *Polyporus* (*Melanopus*) *squamosus*, grown in darkness, bear an astonishing superficial resemblance to those of *Xylaria hypoxylon*.

5. SEXUALITY

A wide variety of sexual forms results from regressive sexual evolution, in contrast with the morphological complexity of many fungi.

Furthermore, fungi exhibit phenomena which are entirely peculiar to themselves, particularly as regards the dicaryophase and tetrapolarity.

(a) **Dicaryophase.** It will be seen that the dicaryophase, a period in diplophase characterized by the dicaryon stage, occurs only in fungi and moreover only in certain groups (Basidiomycetes and some Ascomycetes). It is unknown in Algae, Bryophyta, Pteridophyta, Spermatophyta and animals in general. In these latter organisms there is not the delay in caryogamy which causes the dicaryophase, but, whenever nuclei of opposite sex meet, they fuse immediately to reconstitute a single diploid nucleus with $2n$ chromosomes.

There are, however, exceptions: for example, in Crustaceae there is retarded caryogamy with the formation of a dicaryon in the case of fertilization of the egg of *Cyclops* (Copepoda). This example, given in Wilson's book,¹ was reported in 1900 by Maire.² In the egg of this copepod

¹ Wilson, C. B., *The cell in development and inheritance*, 3rd ed. (New York, 1928).

² Maire, R., L'évolution nucléaire chez les urédinées et la sexualité, *C.R. Congrès internat. Bot.*, Paris, 1900, pp. 135-50.

fusion of the chromosomes is delayed after union of the male and female pronuclei: these associate in the resting stage, but remain separate, then divide simultaneously forming a single mitotic figure in which each nucleus retains its individuality. True fusion occurs only after a series of divisions. In this example, the two groups of chromosomes are reunited in the same nuclear membrane, whereas in dicaryotic fungi the two nuclei retain their individual membranes.

(b) **Tetrapolarity.** It will be seen, when studying sexual polarity, that the existence in heterothallic Hymenomycetes and Gasteromycetes of tetrapolar species is typical of these groups of fungi, and unique in living organisms. If the conjugations between four characteristic compatibility groups of tetrapolar species are really a question of sex, it follows that besides normal sexuality (bipolar or double, with two sexes, male and female, or + and -), there occurs quadruple sexuality, with four "sexes" or mating types in complementary pairs, for which there is no designation and which correspond to nothing else that is known. These remarkable facts may be reproduced and verified by repeating the experiments of Vandendries or Quintanilha, to quote only more recent work. However astonishing or bizarre these facts may appear to be and whatever their possible explanations they imply that the fungi are organisms which are sexually quite distinctive.

COROLLARY

All of these characteristics clearly separate fungi from algae, which also have a thallus, but which also contain chlorophyll; they also separate fungi from bacteria, Schizomycetes, which in general do not form true filaments, do not possess a branched thallus, and in which there is no typical nucleus.

Furthermore, these characteristics permit inclusion among the fungi of certain groups which other authors have excluded.

First of all there are the Myxomycetes, organisms possessing characteristics of both protozoans (mobile plasmodial vegetative structure, motile flagellate zoospores, giving myxamoebae amoeboid movements) and fungi (transformation of the plasmodium into sporangia). The Myxomycetes, in short, are fungi in which the cytoplasmic mass is not enclosed in a hyphal network, but remains exposed in the form of plasmodia.

Gäumann united, under the name Archimycetes, several groups of organisms whose classification is debatable. These are: Olpidiaceae, Synchytriaceae, Plasmodiophoraceae, and Woroninaceae. These families form four independent groups, exhibiting affinities with protozoans, flagellates and Myxomycetes. The Olpidiaceae and Synchytriaceae are sometimes included with the Chytridiales. If fungi are regarded as protista, it is natural to include the Archimycetes, although their thallus is naked for the greater part of their life cycle.

The question is more difficult for the Microsiphonae or Actinomycetes: in works on bacteriology they are included with bacteria, or rather with

Schizomycetes, as the order Actinomycetales; parasitologists, following Vuillemin, prefer to include them in fungi, from which, however, they differ greatly.

Apart from the Microsiphonae, we here adopt for the fungi Gäumann's classes: 1. Archimycetes, with which we include the Myxomycetes; 2. Phycomycetes; 3. Ascomycetes; 4. Basidiomycetes; and 5. Adelomycetes¹ or Fungi imperfecti.

The Adelomycetes, often neglected in textbooks², are nevertheless an interesting and important group. The main attempts at classification are those of Saccardo, in the *Sylloge fungorum* (1886), of Potebnia³ (1910), and of von Höhnelt⁴ (1923) and particularly of Vuillemin.⁵

B. MYCOLOGICAL SYSTEMATICS

The following classification appears to have much practical value. The genera and species parasitic on man and animals are given in heavy type. A sequence of progressive complexity has been adopted, but this implies neither a linear series nor any hierarchy.

1. MICROSIPHONAE OR ACTINOMYCETES

The Actinomycetes occupy an intermediate position between the bacteria, which they resemble in certain forms (bacilli, cocci) and the width of their filaments (1μ), and the fungi, in possessing a branched thallus.

The classification given here was proposed by Waksman and Henrici in 1943 and is favoured by many workers. This classification is outlined as follows.

Order Actinomycetales

A. Family Mycobacteriaceae Chester.

Mycelium rudimentary or absent.

Genus *Mycobacterium* Lehman and Neuman.

Acid-fast organisms belonging to the sphere of bacteriology and not of mycology.

B. Families Actinomycetaceae and Streptomycetaceae.

A true mycelium is present.

I. Family Actinomycetaceae Buchanan.

The vegetative mycelium fragments into bacilliform or cocciform cells.

¹ This term (*ἀδηλος*, uncertain) was proposed by Mangin and Vincens (*Bull. Soc. mycol. France*, **36**, 89-97 (1920)) to designate the Fungi Imperfecti, of which the Hyphomycetes (conidial forms with free conidiophores) comprise only one order, the two others being the Melanconiales and the Sphaeropsidales.

² Gäumann (*Vergleichende Morphologie der Pilze*) gives them 4 pages and 3 figures in a work of 701 pages and 406 figures; Gwynne-Vaughan a single page in a volume of 232 pages; and Bessey, 55 pages out of 791 (1950 ed.).

³ Potebnia, A. A., Beiträge zur Mikromycetenflora Mittel-Russlands, *Annales mycologiques*, **8**, 42-93 (1910).

⁴ Höhnelt, F. von. System der Fungi imperfecti, *Mykol. Untersuch.*, **1**, 301-403 (1923).

⁵ Vuillemin, P., Matériaux pour une classification nationale des fungi imperfecti. *C.R. Acad. Sci., Paris*, **101**, 882 (1910); Les conidiospores, *Bull. Soc. sci. Nancy*, (3), **11**, 129-72 (1910); Les aleuriopores, *Bull. Soc. sci. Nancy*, (3) **12**, 151-75 (1911).