

INTRODUCTION TO MYCOLOGY

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By

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PREFACE

THE development of botanical studies during the past fifty years reflects an expanding specialization in many aspects of the science. This tendency has been very evident in mycology due to an increasing awareness of the part played by fungi in human economy both as ally and as foe which has resulted in exploitation on the one hand and in opposition on the other, to a rapid extension of our knowledge of the structure and life-cycles of individual species, and to the discovery of a wide range of new species. Not only has mycology emerged as a special discipline within botany but also it has become split up into particular disciplines within the whole. The student essaying into mycology is embarking on a study as wide in its scope as any in the realms of Natural Science. Almost at once he is brought face to face with the special interests of individual mycologists as displayed in their writings which inevitably disclose, to a varying degree, the personal predilections of the authors, and rightly so, because the field is now so vast that a synthesis of the whole would be an impossible task for any single author.

It is essential that the student, coming for the first time into contact with mycology, should be introduced to the living entities, which are the fungi themselves, but, what is even more important, he should be introduced to the fungi as entities within the habitats in which they normally exist. It is only along this way that he may be led to realize that the species inhabit locations where they may be sought, may be examined as their life progresses from stage to stage, may be recognized by characters peculiar to each individual and, if desired, may be disposed in a classification which should allow ease of reference however it may reflect personal idiosyncrasies. It is the whole individual which counts and this fact must at all times remain in the forefront of the student's mind even when later he becomes interested in particular facets of the life-cycle of individuals. The part should never be allowed to dominate the whole.

Preface

The introduction to mycology is an important phase in the education of the student even though he may not finally specialize in this aspect of botany. It will be possible to present only certain facts selected from a wealth of material and this selection is bound to show traces of a teacher's or an author's personal interests. Later fresh aspects of the subject will be studied, new and more mature values will be developed which will extend and amplify, will revise and rearrange, the information presented in any introductory course, but it is in this course that the foundations are laid and these must be soundly laid.

Dr. Macdonald has approached the production of an Introduction to Mycology in a realistic manner, recognizing that much must be excluded to be left to a more advanced stage in the student's career. Further, he has dealt with individuals, with "types", the vast majority of which, in all their stages of growth, are within the purview of students starting on a course of botany. I believe the concentration on the individual species, and on its life-cycle, to be sound, the more so as this life-cycle is unfolded against the background in which the species lives. That many of the species are parasites reflects the choice of the author and does not detract from the instruction of the student because it permits of a gradual advance from the obvious to the less obvious as the range of knowledge and the experience of the student expands.

I believe this work should appeal to all students of botany, and in particular to those who wish to specialize in mycology in their later years, but it is written in a manner which brings it within the scope of the upper forms of schools and of the interested lay reader.

*University of Nottingham
July, 1951*

C. G. C. CHESTERS

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AUTHOR'S NOTE

PROBABLY the best introduction to a study of the fungi is to read one of the shorter semi-popular accounts, such as that contained in *Fungi* by Ramsbottom (1929). From such a work to any of the standard mycological text-books is a very long step. Students using even the best of these are bewildered by the diversity of phenomena and the mass of examples therein described. There seems to be a need for an account of the fungi which is rigorously restricted to dealing with the major phenomena in general terms and which illustrates them by reference to a limited number of examples. This book is intended to supply such an account. Further, reference to original papers has been limited almost entirely to a few of the most recent which have not yet been noticed in the better-known mycological text-books. The more advanced student will, inevitably, turn to the fuller discussion contained in more advanced works referred to in this text. There he will find the original sources listed in detail. He will be able to seek out the papers dealing with aspects of mycology which interest him. This book is intended to supply a straight and perhaps artificially easy main road to an understanding of mycology. It only signposts the many intriguing byways.

The subject of plant disease is introduced because it is so closely linked with an understanding of the life histories of so many fungi. The industrial and medical aspects of mycology are scarcely mentioned. The plant viruses and bacteria have been excluded regretfully as outside the scope of this book. For information on these subjects the reader is referred to the works of the following authors:—Plant diseases, Bawden (1948), Butler and Jones (1949); medical mycology, Lewis and Hooper (1943), Dodge (1935); industrial mycology, G. Smith (1946); plant viruses, K. M. Smith (1948); bacteria, Dowson (1949), Bisset (1950).

My very sincere thanks are due to all those publishers, editors and authors who have given permission for the reproduction of illustrations. Acknowledgment of the

Author's Note

source is made under all such drawings. I am deeply indebted to Professor Chesters for his interest in my book and for his many helpful suggestions.

University of St. Andrews
July, 1951

J. A. MACDONALD

INTRODUCTION

THE TRUE fungi were placed by Eichler (1886) in one class of the division Thallophyta of the Cryptogamae. This division contains those plants in which the vegetative body is not differentiated into root, stem or leaf and is described as a thallus. Modern views on their relationships with other groups and among themselves will be discussed later. The study of the fungi, often only from the point of view of their edibility or otherwise, has been going on since Roman times. Early descriptions are purely morphological. Works on the fungi prior to the 18th century are now of interest mainly on account of their illustrations of the gross morphology of species. These are often both beautiful and accurate. In the early 18th century, however, Micheli (1729) made microscopical examination and gave careful descriptions of many species and even did some culture work with moulds. By the early 19th century, so many fungi were described, and often the same fungus by so many different names, that the work of Fries in his "Systema Mycologicum" (1821-32) was very valuable in making clear the widespread synonymy as well as in adding the description of many new species. Fries' "Systema" is accepted as the starting point for modern nomenclature in most groups of the fungi. In the 19th century attention was turned to many of the microscopic fungi and these were described as well as the larger forms, notably in the brilliantly illustrated "Selecta Fungorum Carpologia" of the brothers Tulasne (1861-1865). The culmination of all this descriptive work was the massive twenty-five volume "Sylloge Fungorum" of Saccardo, published between 1882 and 1931. This contains descriptions of all fungi known at that time with diagnoses, synonymy, distribution notes, etc. In the 19th century, too, de Bary investigated the life histories of many fungi. The extent and

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importance of his work is shown in its translation from the German as "Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria" (1887). His influence on his school was profound. From their work developed the use of pure culture methods as an indispensable tool in the study of the fungi. In this connexion the work of Breseld (1872-1912) was outstanding. The foundation was thus laid for the cytological studies which began at the close of the century, under workers such as Dangeard (1889-1907), which have multiplied during the first half of the 20th century and have stemmed into much work on the genetics of the fungi.

The study of any group of organisms must begin with a consideration of their nomenclature. The starting point for the naming of many groups of plants is Linnaeus's "Species Plantarum" (1753). Linnaeus in this work adopted the binomial system of nomenclature by which every plant bears a Latin name made up of two parts. The first is a noun indicating the genus to which it belongs, the second the specific epithet which is an adjective. It is desirable, but, unfortunately not essential, that both words should indicate something of the affinities and appearance of the plant which they specify. Many names of genera and species are given in honour of people or places and so are valueless as clues to the establishment of the identity of the organisms to which they refer.

In every plant binomial the first word is written with a capital letter. The second may be so for a variety of reasons, such as the honouring of a distinguished botanist, e.g. *Pythium de Baryanum* after de Bary. There is a strong move towards writing all specific epithets with a small letter. This method is followed in this book.

Till 1910 the nomenclature of the fungi was accepted as starting with Linnaeus's work. In that year the Third Botanical Congress at its meetings in Brussels drew up rules for the naming of fungi. These rules have been revised and extended at subsequent conferences. At any time there are always some recommendations on nomenclature which are

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on trial. Thus, complete uniformity in usage is never attained. Briefly, it was decided in 1910 that the starting dates and authorities for the naming of the Fungi and related forms should be

- Myxomycetae 1753 Linnaeus "Species Plantarum."
Lichenes 1753 Linnaeus "Species Plantarum."
Fungi (i) Uredinales, Ustilaginales, Gasteromycetales
1801. Persoon "Synopsis methodica Fungorum."
(ii) All other groups
1821-1832. Fries' "Systema Mycologicum."

To take one example, these rules mean that a name given to one of the Uredinales (rust fungi) prior to 1801 is invalid, unless it is the name accepted by Persoon in his "Synopsis." For any rust fungus described for the first time after 1801 the correct name is the earliest valid name by which it has been called. In some cases names which are not valid in accordance with a strict application of the rules are so well established that their use is generally agreed upon.

Cases of synonymy are very frequent. They are particularly common and confusing where the fungus concerned has a number of distinct stages in its life cycle, each of which may at one time or another have been given one or more different names by different workers. Thus *Puccinia graminis* has 12 synonyms, according to Saccardo (1888).

In all plant nomenclature the name of the worker who first published a diagnosis of the species is quoted after its specific name. *Puccinia graminis* Pers. was first validly so called by Persoon. Where the name of one authority following that of the fungus is bracketed and succeeded by the name of a second authority, as in *Claviceps purpurea* (Fr.) Tul., the meaning is that the first authority (Fries) first described the species, while the second authority (Tulasne) transferred the species from a former to the present genus.

As with other groups of plants, family names normally end in "aceae," e.g. *Pucciniaceae*, and ordinal names in "ales," as in *Uredinales*.

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The recommendations with regard to classes and subclasses of the fungi would give to the names of both types of group the same termination. Thus, commonly, one of the four main divisions of the fungi is named the Phycomycetes (algal-like fungi). This in its turn is subdivided into Oomycetes and Zygomycetes. This makes for confusion. For this among other reasons the name used for the algal-like fungi in the following pages will be Phycomycetae. The same termination is applied to the names of the other three main divisions of the fungi, viz. Ascomycetae, Basidiomycetae and Deuteromycetae. This is the nomenclature adopted by Smith (1938).

2

GENERAL

THE FUNGI are a very old group. Undeniably fungus remains, resembling the non-septate hyphae and thick-walled resting spores of modern members of the Phycomycetae, have been found in 300 million-year-old Middle Devonian strata in the Rhynie Chert in Aberdeenshire, Scotland. The name *Palaemyces* has been given to these fossil fungi. They are associated with and apparently parasitic on members of one of the oldest known groups of the Pteridophyta—the Psilophytales.

A conservative modern estimate places the number of the fungi at 40,000 (Bisby, 1945).

All fungi are entirely devoid of chlorophyll. They must, therefore, live either as saprophytes or parasites. They cannot utilize directly the energy from the sun. Supplies of energy to enable them to carry on their life processes have to be obtained indirectly from organic food materials, in which this solar energy has already been stored. All

General

fungi are capable of breaking down such complex, solid, organic foods into comparatively simple substances in solution. These latter they absorb and use as sources of energy in their life processes. Thus *Polyporus betulinus* Fries, one of the bracket fungi attacking birch trees, will reduce the weight of the standing tree by as much as 60 per cent, and finally cause the attacked timber to disintegrate into powder. To enable them to effect these breakdowns saprophytes and parasites alike possess a battery of enzymes capable of acting on insoluble carbohydrates, proteins and fats and converting them into soluble, absorbable substances. The presence of eight such enzymes has been demonstrated in *Polyporus betulinus* by making extracts of the juices of its bracket-shaped fructifications. Twenty-one enzymes have been shown to be present in *Lenzites saeparia* Fries, another wood-destroying fungus, occurring on coniferous timber.

Certain growth factors, some of which may be identified with vitamins, must be present before normal growth will take place in fungi. These growth factors affect such phenomena as respiration, reproduction and growth rate. Three whose presence has been shown are vitamin H (biotin), vitamin B₁ (thiamin) and vitamin B₆ (pyridoxine). Some act as co-enzymes and are essential to the chemical syntheses which fungi bring about.

As with other plant groups, direct evidence of synthesis of food materials within the fungus body is difficult to obtain. That such synthesis does take place is amply demonstrated, however, by the presence in the thallus of the complex carbohydrate glycogen, of protein crystals and of oil drops.

With regard to organic nutrition, carbohydrates are most important as sources of energy, but proteins and fats also play their part.

Sugars such as glucose and sucrose are used as sources of carbon and even polysaccharides may be employed. Radioactive carbon (C^{14}) has been experimented with to prove that some fungi may utilize directly carbon dioxide for the building up of cellular material and organic acids.

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Depending on the fungus, nitrogen may be used as organic nitrogen, ammonia or inorganic nitrogen, or in the first two or in all three of those forms. Some fungi can even fix nitrogen, as well as making use of it in one or other of the combined forms. Mix (1951) has reported that of thirteen species of yeasts in the genus *Torulopsis* nine utilized the eight ammonium compounds, five nitrates and twenty amino acids or related compounds which they were offered, while four others showed varying degrees of selectivity. In *Taphrina* fourteen forms of *T. caerulescens* from different hosts varied as much in their behaviour as did separate species.

As far as the mineral nutrition of the fungi is concerned, it appears that potassium, phosphorus, magnesium and sulphur are the most important and probably essential elements to most species; while the presence of iron, copper, manganese, zinc and possibly calcium stimulates the growth of at least some.

The balance between the active and resting vegetative phases and between vegetative and reproductive stages is governed by physiological factors and swayed by their variation. For example, the pH of the external medium and the food materials which it provides affect the growth of all fungi profoundly and different species react differently to the same environment. External stimuli such as light may affect profoundly both the direction and nature of the growth of fungi. The physiology of the fungi is dealt with fully by Hawker (1950).

Owing to their parasitic or saprophytic habit, the fungi do not need to spread out their thalli to light; but must ensure that they are brought into intimate contact with their source of manufactured food. The vegetative stages of most fungi are, therefore, produced buried in the substratum on which they grow. The great majority of toad-stools, for example, form the spreading threads of their thalli below the soil surface, the reproductive fruitbodies alone appearing above ground.

The vegetative thallus typically consists of branching tubes or threads called hyphae. These tubes are composed

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of living protoplasm contained within a wall. The tube may be without transverse septa as in the Phycomycetae (Fig. 1). Protoplasmic streaming is readily detected in the hyphae of

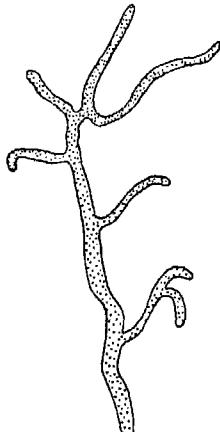


Fig. 1. Coenocytic mycelium of a Phycomycete

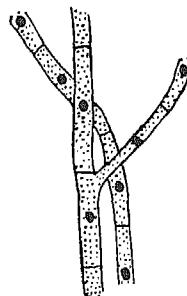


Fig. 2. Septate mycelium of an Ascomycete

members of this group. There are transverse septa in the Ascomycetae, Basidiomycetae and Deuteromycetae (*Fungi Imperfecti*) (Figs. 2, 3). The threads have definite, apical meristematic regions which may be limited to $10\ \mu$ in length (Macdonald, 1949). The development of the thallus may be limited. In some *Taphrina* species (Exoascaceae) it is

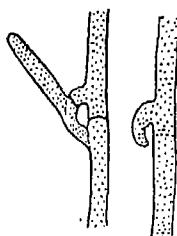


Fig. 3. Septate mycelium of a Basidiomycete, showing clamp connexions

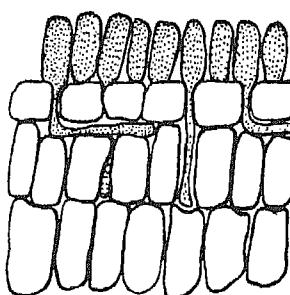


Fig. 4. Intercellular mycelium of *Taphrina*, restricted to the spaces above and between the palisade cells

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confined to the intercellular spaces in restricted regions of the leaves of the host plant (Fig. 4). In certain yeasts (*Saccharomycetaceae*), the thallus consists of a single uninucleate, more or less spherical cell (Fig. 5). In the family *Synchytriaceae*, it may fail altogether to assume the filamentous form.

The cell wall is composed of carbohydrate material. This is predominantly cellulose in many of the lower fungi (*Phycomycetaceae*). The wall may also contain callose, pectose and related compounds. Usually, it does not give a blue

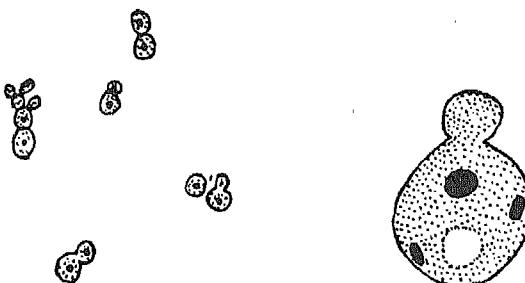


Fig. 5. Uninucleate, spherical Yeast cells, some of which are joined together in chains

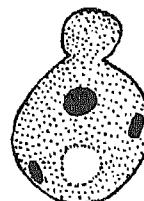


Fig. 6. Yeast cell showing single nucleus, cytoplasmic granules and a vacuole

colour reaction when treated with iodine and sulphuric acid. In the higher fungi (*Ascomycetaceae*, *Basidiomycetaceae*) the wall consists mainly of fungus cellulose. This contains cellulose with additional strengthening material which is nitrogenous in character and is allied to the chitin of insects.

As a rule plastids are absent from the cytoplasm. There are various types of crystals and granules present, for example angular protein granules occur in the cells of brewer's yeast (Fig. 6). Starch is not formed by the fungi. Storage materials include a number of carbohydrates particularly glycogen. This is readily transformed into sugars. Proteins and oils are also stored.

Filaments are aseptate (coenocytic) containing numerous nuclei, or are divided by transverse septa into cells containing

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single or several nuclei. In most cases nuclear division takes place unrelated to wall formation. It is generally reported to be otherwise similar to that taking place in the vegetative cells of higher plants. However, many of the fungi have nuclei which are so extremely small that it has not been found possible to make out the details of division.

In many of the Basidiomycetae clamp connexions are formed. These consist of outgrowths from the hyphae which

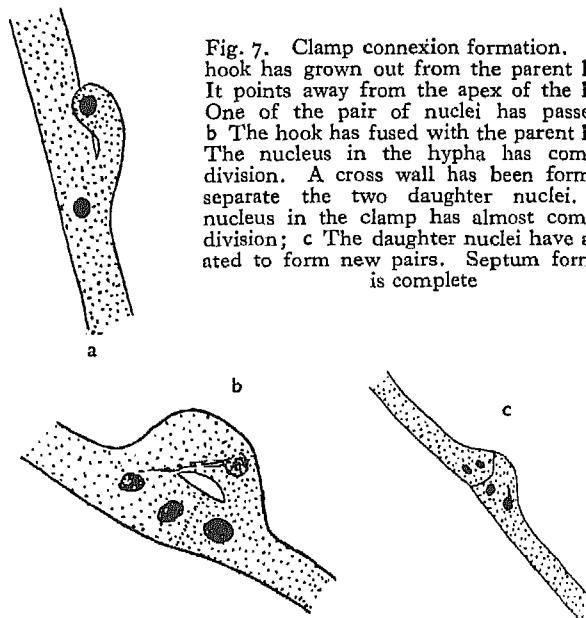


Fig. 7. Clamp connexion formation. a The hook has grown out from the parent hypha. It points away from the apex of the hypha. One of the pair of nuclei has passed in; b The hook has fused with the parent hypha. The nucleus in the hypha has completed division. A cross wall has been formed to separate the two daughter nuclei. The nucleus in the clamp has almost completed division; c The daughter nuclei have associated to form new pairs. Septum formation is complete

make their appearance in a lateral position some short distance behind the end of the terminal segment, e.g. approximately 100μ ($1/10$ mm.) behind the tips of the hyphae in *Marasmius androsaceus* Fr. (Macdonald, 1949). They rapidly assume a hooked shape, curving backwards to rejoin the parent hypha immediately behind their point of origin (Fig. 7a, b, c). More or less simultaneously with this, one cross wall is laid down in the parent hypha opposite the clamp connexion and another is formed in the clamp

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connexion itself. Nuclear division takes place at this time and is said to be associated with the formation of these septa in the way normal to higher plants (Noble, 1937).

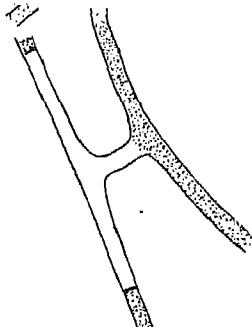


Fig. 8. Hyphal anastomosis in *Typhula gyrans* (Macdonald, 1934)

The use of modern tools such as the phase contrast and reflecting microscopes should make the study of cytology in the fungi easier and lead to an early solution of many problems.

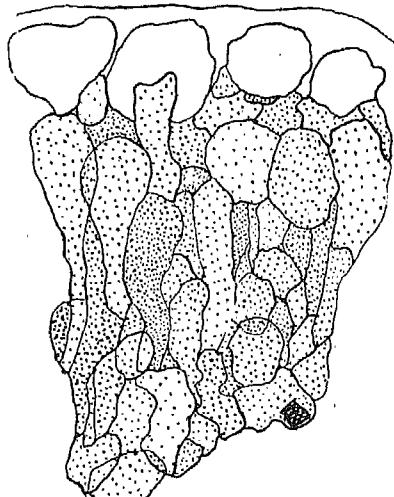


Fig. 9. Pseudoparenchyma formed in connexion with sclerotium formation in *Polyporus betulinus* (Macdonald, 1937)

The mass of threads or hyphae which makes up the vegetative body is called the mycelium. In many fungi the mycelium does not have a definite shape but spreads freely

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over and in the substratum on which the organism is growing. The threads usually branch freely and may anastomose (Fig. 8). Apparently, there is free interchange of contents between the segments of the hyphae which join in this way.

In Ascomycetae and Basidiomycetae hyphae may become very closely intertwined forming a tissue which consists of hollow tubes running in all directions; but which, in transverse section, looks like the cellular parenchyma tissue of higher plants. This is called pseudoparenchyma (Fig. 9).

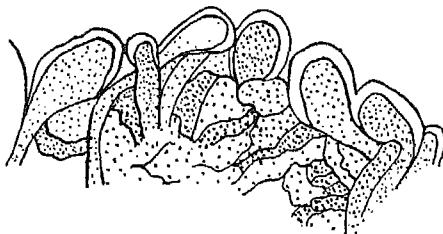


Fig. 10. Development of sclerotium of *Typhula gyrans*, showing formation of the rind layer (Macdonald, 1934)

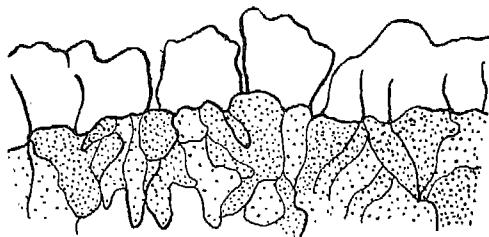


Fig. 11. Mature sclerotium of *Typhula gyrans*, showing thickened rind (Macdonald, 1934)

The pseudoparenchyma may take the form of a roughly rounded body with a specialized outer limiting layer consisting of the tips of hyphae which have become thickened and are usually dark brown or black in colour. This structure forms a resistant, resting stage for the fungus and is called a sclerotium (Figs. 10, 11). Sclerotia of this kind are common. They occur for example in the genus *Sclerotinia* among the Ascomycetae, in *Typhula* and *Polyporus* among Basidiomycetae and in *Sclerotium* among Deuteromycetae. Sclerotia vary in size from less than 1 mm. in diameter upwards. In *Poria (Pachyma) cocos* the sclerotium may reach

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the size of a human head and may weigh up to 16 Kg. Sclerita may be formed freely, on the surface of, or embedded in, living or dead plant or animal tissues. Examples of this

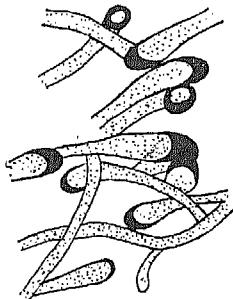


Fig. 12. Black Line hyphae from a culture of *Polyporus betulinus* (Macdonald, 1937)

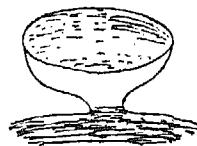


Fig. 13. Diagrammatic drawing of a short-stalked apothecium

latter condition occur commonly among the bracket fungi which grow on trees. In such cases the infected area or areas may be bounded by a dark line. This consists of hyphal

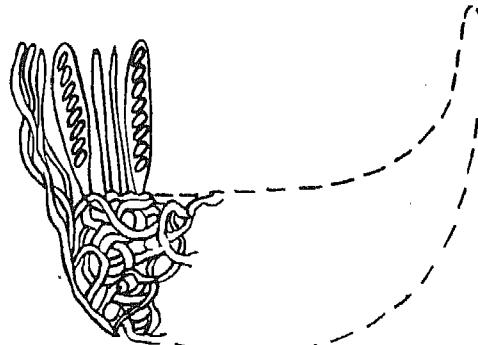


Fig. 14. Diagrammatic drawing of a section through an apothecium

portions similar in appearance to those forming the rind of a true sclerotium (Fig. 12). The area which they enclose certainly represents the limit of spread of the fungus at the end of some period of its growth. The name pseudosclerotium has been used to describe these areas.

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There is a tendency, which becomes increasingly obvious among the higher fungi, to develop dense masses of hyphae in relation to the formation of the reproductive stages. The term stroma is applied to these hyphal aggregates. The open, spore-producing layer of the fructification (apothecium) of the cup fungus, *Peziza*, is based on such a dense mass of pseudoparenchyma (Figs. 13, 14). In *Claviceps purpurea* (Fries) Tul., the Ergot Fungus, an elongated, resting sclerotium is formed which later gives rise to drum-stick

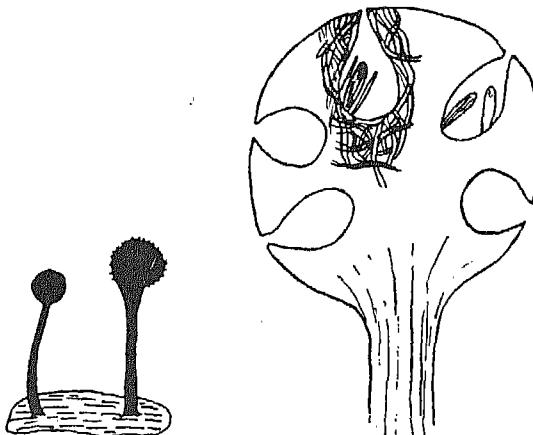


Fig. 15. Diagrammatic drawing of two stromata containing perithecia

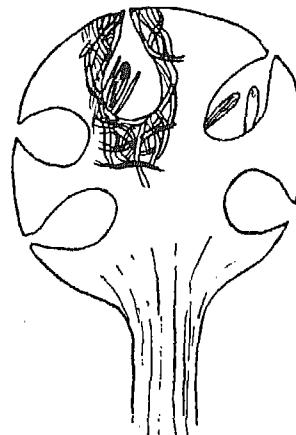


Fig. 16. Diagrammatic drawing of a vertical section through a stroma containing perithecia

shaped stromata containing closed, flask-like fructifications (perithecia) embedded in the heads (Figs. 15, 16). The fructifications of some bracket fungi on trees and of *Xylaria polymorpha* (Pers.) Grev. are often formed associated with pseudosclerotia buried in the wood. The pseudosclerotia might then equally well be called pseudostromata.

Sometimes, among the Basidiomycetae, individual hyphal threads twist round each other to form long mycelial strings or cords. These can be found by digging carefully in the uppermost few inches of the leafy soil in many woodlands. The mycelial strings are white in colour, as a rule, and are,

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therefore, readily seen. These strands are called rhizomorphs. In a few cases the mycelial cord is surrounded with a dark rind similar to that which surrounds a sclerotium. The rind gives to the cord a tough, root-like character. This is so in the Honey Fungus, *Armillaria mellea* (Fr.) Quél., one of the most ubiquitous fungus parasites known (Fig. 17). In the Heather Rhizomorph Fungus, *Marasmius androsaceus* Fries, the rhizomorphs may be as fine as hairs (Macdonald, 1949) (Fig. 18).

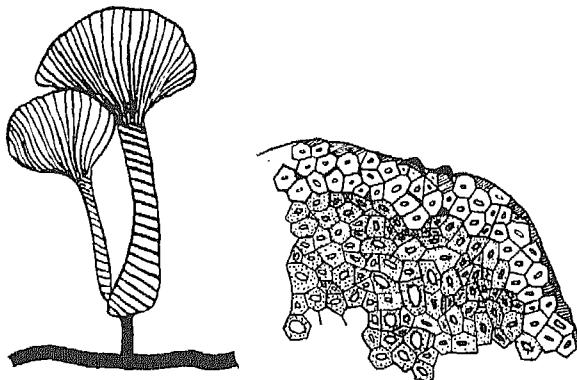


Fig. 17. *Armillaria mellea*, the Honey Fungus, Toadstools arising from a branch of a rhizomorph (adapted from Hiley, 1919)

Fig. 18. Section through a rhizomorph of *Marasmius androsaceus* (Macdonald, 1949)

In addition to spreading by means of the mycelium or by one of its specialized forms, fungi reproduce themselves by a wide variety of both vegetative and sexual spore forms. Vegetative spores may be formed inside sporangia and be motile, e.g. *Saprolegnia* (Fig. 19), or non-motile, e.g. *Mucor* (Fig. 20). The whole sporangium may function as a single spore as in *Peronospora* (Fig. 21). Sometimes the mycelium breaks up into rounded portions to which the name gemmae is given. The yeasts are regarded as reduced fungi of this type (Fig. 22), in which the mycelium has entirely broken up into such portions. In other cases characteristically-shaped buds

General

are formed, like the chains of barrel-shaped spores in the Powdery Mildews (Fig. 23). Thick-walled, resting cells make their appearance in the hyphae of many fungi as in *Mucor ramannianus* Möller (Fig. 24). They become separated when mature and are, therefore, a means of reproduction as well as

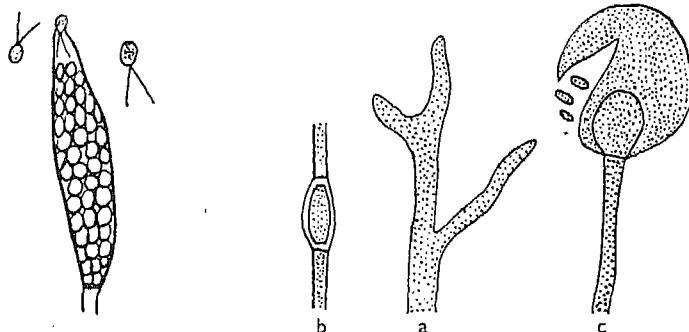


Fig. 19. *Saprolegnia*. Sporangium with motile spores

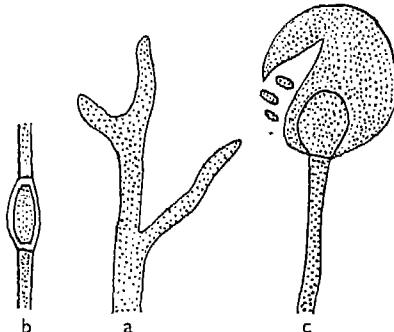


Fig. 20. *Mucor*. a Non-septate hypha, b hypha with chlamydospore, c Sporangium with non-motile spores (after Campbell, 1938)

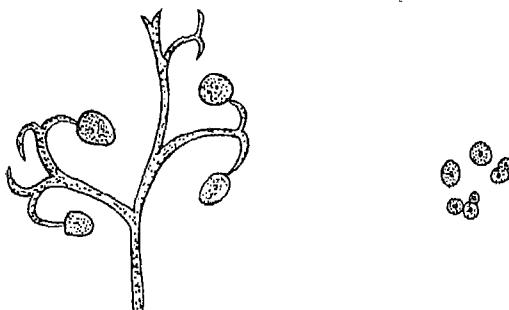


Fig. 21. *Peronospora*. Sporangium which functions as one spore

Fig. 22. *Saccharomyces*. Yeast cells budding

of survival. It is not uncommon for the same fungus to reproduce by several different vegetative means.

In addition to the production of vegetative spores, it is an almost universal phenomenon in the fungi for spores to be formed sexually. This follows the fusion of nuclei which are contained in, or derived from, clearly-differentiated

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reproductive organs: or follows the fusion of nuclei contained in hyphae which are indistinguishable from ordinary vegetative ones, yet which are believed to be derived from

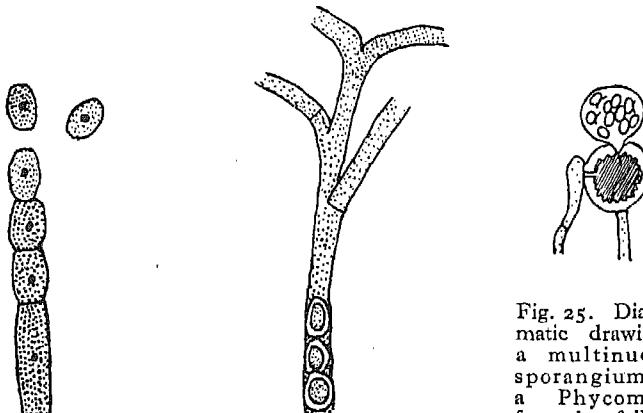


Fig. 23. *Erysiphe*.
A Powdery Mildew
producing un-
branched chains of
barrel-like spores
(conidia)

Fig. 24. *Mucor ramanianus*. Hyphae
with thick-walled
chlamydospores (after
Campbell, 1938)

Fig. 25. Diagrammatic drawing of a multinucleate sporangium of a Phycomycete formed following the fusion of the reproductive organs. This sporangium has liberated its spores into a vesicle above

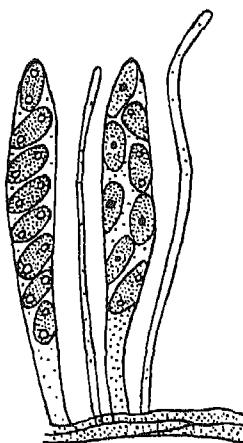


Fig. 26. Sporangium (ascus)
of an Ascomycete containing
8 ascospores

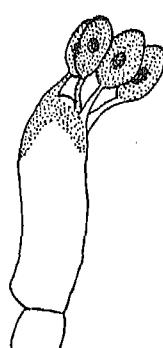


Fig. 27. Sporangium (basidium)
of a Basidiomycete
bearing 4 basidiospores

Classification

such reproductive organs. The form of the organs when present and the manner of the fusion varies between and within the main groups. It will be dealt with more fully under each group. In the Phycomycetae the direct product of the fusion of the reproductive organs is always a uninucleate or multinucleate sporangium which ultimately liberates its spores (Fig. 25). The sporangium typically contains eight spores, in the Ascomycetae (Fig. 26); in the Basidiomycetae it bears four spores externally (Fig. 27).

3

CLASSIFICATION

ANY ATTEMPT at a natural arrangement of the families of the fungi presents difficulties. These difficulties are exaggerated if the attempt is made before the families have been discussed. As only a very limited number of examples is described in this book, any discussion of the relationships among the fungi will be confined to general terms. An account of the different views on a natural classification among the groups of fungi and of their relationships with other groups of Thallophyta is postponed till the close of the description of each group.

The following is a grouping of the fungi, dealt with in subsequent pages, which is only semi-natural and should be regarded in the same light as the mechanical keys used to run down specimens of Flowering Plants.

The true fungi are divided into four classes.

With aseptate mycelium

Phycomycetae—The vegetative mycelium is typically aseptate. Cross walls occur only in connexion with the formation of the reproductive organs. Spores are produced

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in indefinite numbers in sporangia. In most species there is fusion between gametes, resulting in the formation of a zygote which is surrounded by a thick wall and germinates only after a resting period.

With septate mycelium

Ascomycetae—The characteristic sporangium, the ascus, is produced after the fusion of gametic nuclei. The fusion nucleus undergoes a reduction division and ultimately the ascus contains, typically, eight spore nuclei, round which are formed the walls of the eight ascospores.

Basidiomycetae—The sporangium here is the basidium which, after the fusion of the two nuclei contained in it during early development and a subsequent reduction division to give four nuclei, produces externally the uni-nucleate spores. These are four in number in most species. The number is indefinite, however, in one group, the Ustilaginales.

Deuteromycetae (Fungi Imperfici)—The species included under this heading have not shown any method of sexual reproduction and have not produced either asci or basidia. Asexual reproduction takes place by conidia. Some, by their method of conidium formation, appear to be imperfect stages of Ascomycetae, others of Basidiomycetae. A few produce no spores at all.

MYXOMYCETAE

As is usual, forms not regarded as being true fungi are dealt with first. The Plasmodiophorales are, however, taken as true fungi and are included with the Phycomycetae near the Chytridiales (Karling, 1942), contrary to the view

Myxomycetae

accepted by Smith (1938) and Gwynne Vaughan and Barnes (1937) which places them in the primitive group Myxomycetae.

The Myxomycetae are rather isolated and curious forms. A popular article in "Life" [April 24th, 1950] gave an outline of the life history of *Dictyostelium discoideum*, which was finely illustrated. It will be sufficient to give a generalized account of their life history, here.

In early stages the organisms appear as small (approximately 5–10 μ), uninucleate, haploid, amoeboid structures called myxamoebae. They possess a contractile vacuole and other vacuoles into which solid food material is absorbed (Fig. 28). The myxamoebae divide repeatedly giving rise

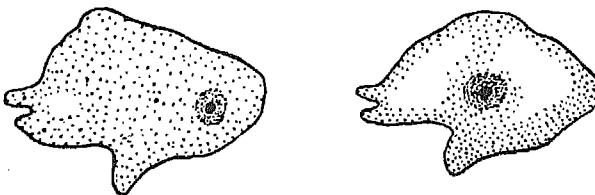


Fig. 28. Myxomycete myxamoebae (adapted from Wilson and Cadman, 1927)

to a large number of individuals. Mitotic nuclear division accompanies the division of the myxamoebae. The individuals formed are converted, in higher forms, into anteriorly-uniflagellate, pyriform zoospores, which retain some capacity for amoeboid movement especially at the posterior end (Fig. 29a). There is a blepharoplast associated with the flagellum. This is a deeply-staining granule (possibly a centrosome), having a direct connexion with the base of the flagellum. If zoospores have been formed these also increase by division. Ultimately, they function as gametes; they fuse in pairs or reassume the myxamoeboid form and then fuse in pairs. Fusion is by apposition of the posterior ends (Fig. 29b). It is not followed immediately by nuclear fusion. The amoeboid zygotes have paired nuclei. In some species there is evidence that the gametes are of two physiologically

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different types; but this is not always so. Other gametes may fuse with the zygote but their nuclei degenerate and are digested by it. This is followed by the fusion of the gametic nuclei (Fig. 30). The fusion nucleus in the zygote divides repeatedly so that the zygote develops into a diploid, multinucleate mass of protoplasm called a plasmodium. Zygotes may come together, or plasmodia may fuse. In

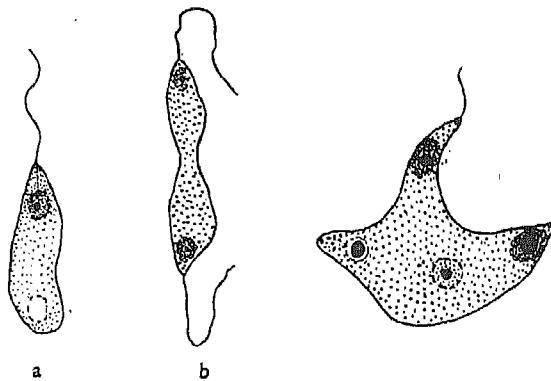


Fig. 29. a Myxomycete zoospore, b two zoospores functioning as gametes and fusing by their anterior ends (after Wilson and Cadman, 1927)

Fig. 30. Myxomycete zygote with single fusion nucleus and degenerating nuclei belonging to other gametes which have fused with the zygote (after Wilson and Cadman, 1927)

either case larger plasmodia are formed. Even large plasmodia may fuse and active growth and nuclear division take place.

The plasmodium flows about over the substratum engulfing solid food particles, spores or myxamoebae which come in its way. It consists of a thin sheet of naked protoplasm with denser strands, in which streaming is well seen. The size varies from a few square inches in most species up to a square yard in *Fuligo varians* Rost. These plasmodia are to be seen on the bark of tree stumps, on stored wood, etc. While growth is active they keep to moist places where light

Myxomycetae

is not strong. The organism may continue in this condition for a year, under favourable circumstances. If exposed to drought, it forms dense masses of thick-walled bodies, to which the name sclerotia has been applied; but will

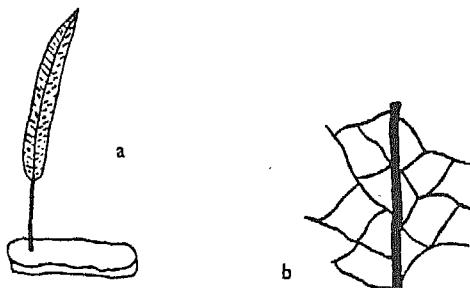


Fig. 31. *Stemonites ferruginea*. a Stalked sporangium; b Capillitium forming tubes

revive quite quickly on wetting after periods up to a year or even, exceptionally, five years. The flowing movement takes place back and fore over the same area. If it is allowed to carry on normally, the plasmodium sooner or later moves

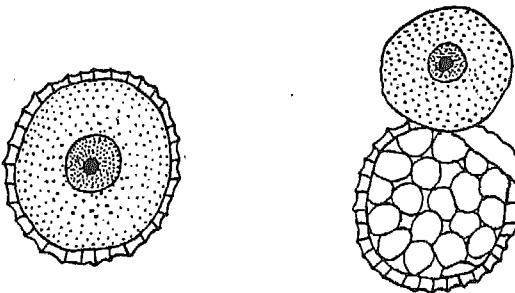


Fig. 32. Myxomycete haploid spore
(after Wilson and Cadman, 1927)

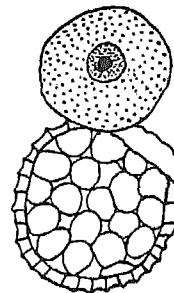


Fig. 33. Myxomycete spore germinating to form a myxamoeba (after Wilson and Cadman, 1927)

to a dryish, well-lighted place and gives rise to protuberances from which sporangia of various shapes are formed singly or in groups. Group formation is due to the plasmodium

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breaking up into fragments during the early stages of sporangial development. The sporangium may be more or less flattened and biscuit-shaped as in *Fuligo septica* (Linn.) Gmel. or reticulate and not unlike the plasmodium as in *Trichia persimilis* Karst. In *Lycogala epidendrum* Fr. it is spherical. In *Stemonites ferruginea* Ehrenb. each sporangium has a thin stalk and a long head (Fig. 31a).

Inside each sporangium a mass of spores develops. Meiosis takes place during the last two divisions of the spore-forming nuclei. In the higher forms the spores are embedded among threads or tubes (elaters) which form the capillitium (Fig. 31b). The hygroscopic movements of these elaters cause the opening of the sporangium. The haploid spores are thus set free. Each gives rise to a myxamoeba (Figs. 32, 33).

5

PHYCOMYCETAE—GENERAL AND CLASSIFICATION

THE LOWEST class of the true fungi is the Phycomycetae, algal-like fungi. Most aquatic fungi and the simplest of the land forms fall into this group. The mycelium is typically composed either of coenocytic filaments or of isolated, more or less rounded cells. It is never compacted into pseudo-parenchyma. Sexual reproduction is by distinct gametes or clearly differentiated sexual organs. Normally, the gametic nuclei fuse in the organ in which they come together.

The Phycomycetae may be divided into nine orders each containing several to many families. A complete analytical key is not given as it does not help to clarify the relationships among the orders. It is possible to construct one (Sparrow, 1943; Fitzpatrick, 1930) by dividing the class into two series

Phycomycetae—General and Classification

based on the presence or absence of swarm spores. Each series is further subdivided either, in the first case, on the possession of a single flagellum or two flagella or, in the second, on whether the sporangium itself functions as an airborne spore or contains non-motile aplanospores.

Such an arrangement has the demerit of separating, mechanically, families which are generally accepted as being closely related, *e.g.* Pythiaceae and Peronosporaceae. It appears to be better, therefore, to retain a more conservative classification which groups the orders into two subclasses, the Oomycetes and Zygomycetes.

The Oomycetes contain seven orders. The first two orders have sexual reproduction by fusion of motile isogametes resembling zoospores, or by union of two similar individuals.

Chytridiales—These are usually one-celled fungi, the whole cell becoming transformed into a sporangium which ultimately sets free zoospores.

The most interesting families are Synchytriaceae and Cladochytriaceae. In the former the thallus (cell) forms a sorus of summer sporangia or resting winter sporangia. Each type of sporangium sets free zoospores. In the latter a mycelium is developed and zoosporangia and resting sporangia are formed.

Plasmodiophorales—This, the second order, contains one family, Plasmodiophoraceae. The forms have a naked thallus and give rise to resting spores which each germinate to produce a zoospore with two unequal flagella.

The other five orders have sexual reproduction involving antheridia and oogonia, that is unequal (dissimilar) sexual organs. Fertilization results in the formation of oospores. Asexual reproduction is either by zoosporangia which set free zoospores, or by entire sporangia which function as single spores (conidia).

Blastocladiales—This order consists of aquatic or soil fungi with rhizoidal thalli. Two generations are produced. One, the asexual sporophyte, bears zoosporangia and resting spores, the other, the sexual gametophyte, bears mono-flagellate gametes of unequal size in separate gametangia on

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the same plant (monoecious condition), or on separate plants (dioecious condition).

Monoblepharidales—These are also aquatic fungi. Asexual reproduction takes place by the production of zoospores.

Sexual reproduction involves the fertilization of the oogonium by a motile male gamete or antherozoid.

Saprolegniales—These are aquatic fungi most of which are saprophytes. Asexual reproduction is by zoospores. Antheridia (often absent) and oogonia are formed. Where fertilization occurs it takes place by means of a fertilization tube. A number of oospores is formed from each oogonium.

Lagenidiales—These fungi are parasitic on algae and on small aquatic animals. The thallus is usually confined to a single host cell. It is septate at maturity, when each segment is either transformed into an antheridium, an oogonium, a zoosporangium, or functions vegetatively, germinating by a germ tube.

Peronosporales—A few species in this order are aquatic and some are semi-aquatic, but they are chiefly land fungi. Some are facultative parasites of plants. Asexual reproduction is by zoospores formed within rounded sporangia. In some higher forms the sporangia act as conidia. Sexual reproduction follows the fusion of antheridia and oogonia. Fertilization takes place by means of a fertilization tube and results in the production of a single oospore.

The Zygomycetes have asexual reproduction by non-motile aplanospores, contained in sporangia, or by conidia. Sexual reproduction is by the fusion of two more or less similar cells (gametangia) to form a zygospore. There are two orders.

Mucorales—These are mainly saprophytic land fungi. Asexual reproduction is usually by aplanospores. Sexual reproduction is usually by fusion of morphologically identical gametangia.

Entomophthorales—These fungi are chiefly parasitic on insects. Asexual reproduction is by conidia. Sexual reproduction is by the fusion of gametangia which are often dissimilar in appearance.

PHYCOMYCETAE—OOMYCETES I

CHYTRIDIALES

Synchytriaceae—*Synchytrium endobioticum* (Schilb) Percival. This is the organism responsible for Wart Disease of potatoes (Fig. 34). When the warty outgrowths formed on the tubers decay in the soil, thick-walled, resting sporangia are set free. These germinate giving rise to a number of posteriorly-uniflagellate zoospores (Fig. 35) which penetrate the potato

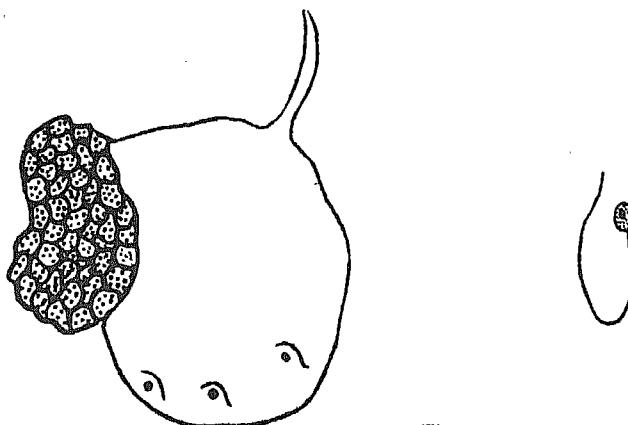


Fig. 34. Potato tuber with wart caused by *Synchytrium endobioticum*

Fig. 35. *Synchytrium endobioticum*. Posteriorly-uniflagellate zoospore (after Curtis, 1921)

tubers at their eyes, lose their flagella and come to lie in the lower half of the infected cells. Each thallus now consists of a naked mass of protoplasm. The attacked cell enlarges and those round about also enlarge, forming a raised portion surrounding the infected cell which lies at the bottom of a depression (Fig. 36). The parasite next surrounds itself with a wall consisting of two yellow-brown layers. This stage is

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called the prosorus. An opening appears in the upper part of the prosorus wall and the protoplasm, which is still uninucleate, passes out into a vesicle or sorus thus forming a rounded mass above (Fig. 37a, b). From repeated division of the single nucleus, four or five multinucleate masses are

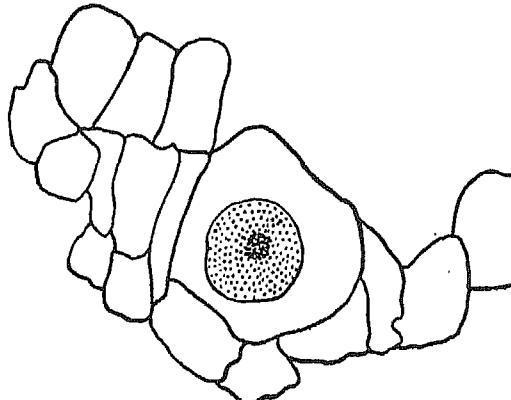


Fig. 36. *Synchytrium endobioticum*. Young prosorus in enlarged, infected cell, at the base of a slight depression in a potato tuber

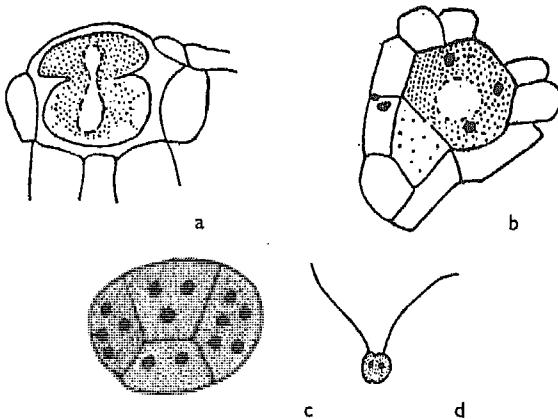


Fig. 37. *Synchytrium endobioticum*. a Prosorus giving rise to a sorus within the same cell; b mature sorus; c walled sporangium from surface of potato tuber; d posteriorly-flagellate zoospores functioning as gametes and fusing laterally (after Curtis, 1921)

Phycomycetae—Oomycetes I

formed. These give rise to walled sporangia which come to lie on the surface of the potato tuber (Fig. 37c). The sporangia set free hundreds of rounded, uninucleate, uniflagellate, motile zoospores. These may either continue to function as zoospores, repeating the type of infection described above and causing increase in the number or size of warty outgrowths on the tubers; or they may function as gametes. In the latter case they fuse laterally in pairs to give a bi-flagellate zygote (Fig. 37d). There is some evidence that the gametes which fuse come from different sporangia. That is

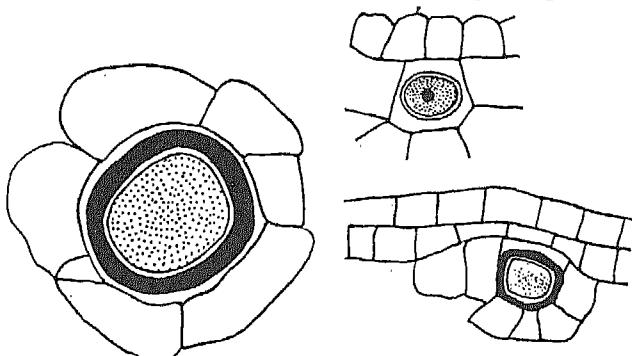


Fig. 38. *Synchytrium endobioticum*. Resting sporangia showing three-layered wall

to say that the pair of gametes differ from each other physiologically in spite of being morphologically identical. Zoospores may be induced to function as gametes by slightly unfavourable environmental conditions, e.g. drying.

This seems to be practically the most primitive type of sexuality, for the cells are morphologically identical, motile and fuse while both are flagellate. They are only potential gametes and may function as zoospores.

A zygospore reinfects in the same way as a zoospore; but the events subsequent to infection are different. The zygospore lies just below the host cell nucleus and causes the host cell to divide by walls tangential to the tuber surface. The parasite always remains in the lower cell so that, as division is repeated, it comes to lie fairly deep in

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the tuber tissue. The naked protoplasm of the parasite becomes surrounded with a thick wall, forming the resting sporangium, which is approximately 52μ in diameter. When mature, the wall can be seen to be made up of two layers, with a third external layer consisting of the wall of the dead host cell (Fig. 38). These sporangia germinate in spring or remain dormant causing the soil to be infective for periods up to ten or twelve years, at least. Prior to germination, the sporangial nucleus divides repeatedly to give hundreds of haploid nuclei, each of which forms a zoospore.

The nature of the life history of the parasite, particularly its ability to survive in the soil for many years, makes the

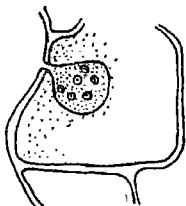


Fig. 39. *Urophlyctis alfalfa*. Infected bud cell of *Medicago lupulina* containing top-shaped mass of protoplasm (adapted from Jones and Drechsler, 1920)

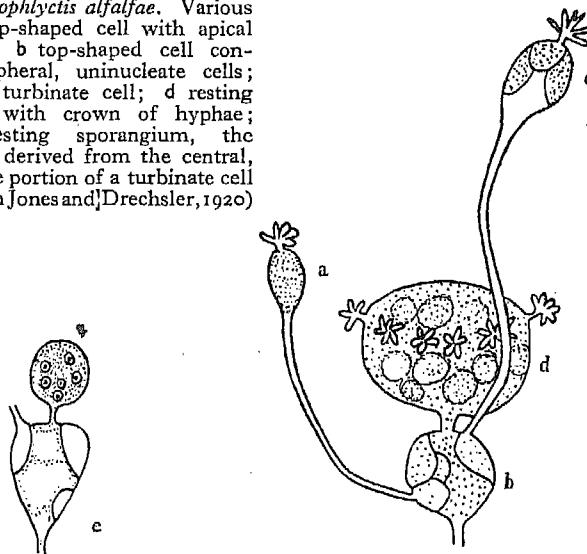
control of wart disease difficult. The problem has been solved by the breeding of commercial varieties of potato which are immune or very highly resistant to the disease. No new variety of potato may be grown commercially in Britain unless it has been tested and proved immune to wart disease.

Cladochytriaceae—*Urophlyctis alfalfa* (Lagerh.) Magn. causes Crown Gall or Crown Wart of lucerne (*Medicago sativa*). It occurs sometimes in Britain. It causes wart-like swellings at the top (crown) of the tap root, and even on the young stem and leaves. The swellings ultimately rot and the death of the young plant is brought about. The decaying host cells contain numerous resting sporangia at this stage. The latter give rise to biflagellate zoospores. One of the flagella is very short. The zoospores are able to infect the buds of a new host plant. Each penetrates an epidermal cell and there produces a roughly top-shaped mass of protoplasm (Fig. 39). Next, the protoplasm becomes surrounded with a

Phycomycetae—Oomycetes I

wall. This top-shaped cell develops a branched, apical haustorium at its broad end (Fig. 40a). Its nucleus divides and some of the nuclei thus formed lie peripherally in the upper part of the turbinate cell giving rise to peripheral, uninucleate cells (Fig. 40b). The remaining part of the turbinate cell is multinucleate. Each of the peripheral cells can develop a long, narrow hypha, which swells at its end within a neighbouring host cell to form another turbinate cell (Fig. 40a, c). By repetition both secondary and tertiary turbinate cells can be formed. Each of the turbinate cells

Fig. 40. *Urophlyctis alfalfaæ*. Various stages: a top-shaped cell with apical haustorium; b top-shaped cell containing peripheral, uninucleate cells; c secondary turbinate cell; d resting sporangium with crown of hyphae; e young resting sporangium, the contents are derived from the central, multinucleate portion of a turbinate cell (adapted from Jones and Drechsler, 1920)



may develop a vesicle which becomes a new resting sporangium. This derives its contents from the multinucleate central portion of the turbinate cell (Fig. 40e). When mature it is a large structure, $30-40 \times 45 \mu$, rather flattened on the side next the turbinate cell. It develops a crown of haustoria similar to the apical haustorium of the original turbinate cell (Fig. 40d). When mature it forms a thick-walled resting sporangium or hypnospore, bearing a ring of scars. On germination this liberates the infective zoospores. There is

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doubt as to whether sexual fusion occurs between pairs of zoospores before infection is brought about.

The gall tissue develops a conducting system of its own due to the conversion of host parenchyma cells into tracheids, which connect up with the normal conducting tissue of the host.

This fungus flourishes in waterlogged soils. It may be controlled effectively by improving drainage.

PLASMODIOPHORALES

Plasmodiophoraceae—*Plasmodiophora brassicae* Woronin causes Club Root or Finger and Toe of many members of the

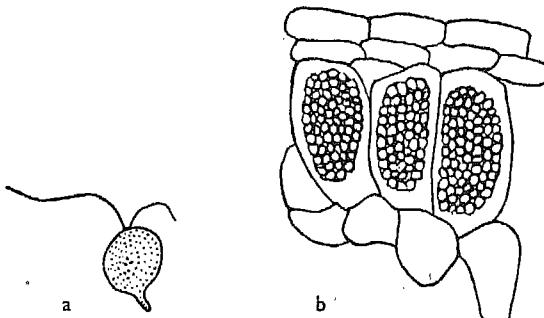


Fig. 41. *Plasmodiophora brassicae*. a Pear-shaped, biflagellate zoospore with unequal flagella (adapted from Ledingham, 1934); b resting spores in cells of turnip root

Cruciferae, particularly commercially important members of the genus *Brassica*, such as turnip, cabbage and cauliflower.

Infection of the host plant takes place in the seedling stage by means of a pear-shaped, biflagellate zoospore with unequal flagella (Fig. 41a). After losing its flagella and assuming an amoeba-like appearance, the fungus penetrates the plant through the root hair or other cell of the piliferous layer, or through wounds. It penetrates as a naked unicellular mass of protoplasm. Once inside, the protoplasm increases in amount. It is known as a myxamoeba. The myxamoebae within the root hairs are easily transformed

Phycomycetae—Oomycetes I

into zoosporangia, each containing 4–8 zoospores. These spores are smaller than the original zoospores. They are set free within the host cells by collapse of the sporangial wall. Some workers consider that they function as gametes, fusing to form a zygote (Karling, 1942). The (zygote) nucleus divides and the organism forms a multinucleate plasmodium. New myxamoebae are budded off. They produce new plasmodia by rapid growth. The presence of the organism stimulates division of both infected and neighbouring cells. The organism is thus distributed and swelling of the host

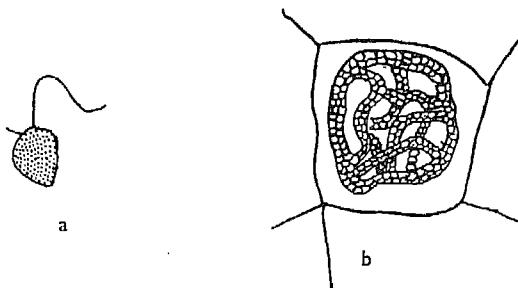


Fig. 42. *Spongospora subterranea*. a Biflagellate zoospore (adapted from Ledingham, 1934); b spongy network of resting spores in cell of potato tuber

tissues results. In cabbage the infection is mainly in scattered groups of cells in the cortex and medullary rays. After a time, the available food is used up. Finally, the plasmodia become segmented into as many portions as there are nuclei. Each resulting uninucleate mass becomes surrounded with a smooth, thick wall and forms a spore, some $2-3\ \mu$ in diameter (Fig. 41b). Those who believe that sexual fusion has occurred earlier, postulate a reduction division immediately prior to spore formation. The spores are set free into the soil by the decay of the attacked tissues. They are capable of immediate germination or of survival in the soil for periods up to eight years. On germination, they produce the biflagellate zoospores.

Plasmodiophora brassicae thrives particularly in acid soils. To control the disease lime may be applied, preferably as

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hydrated lime, at rates up to two tons per acre. On a small scale, mercury salts such as corrosive sublimate may be employed in solution in water. Resistant varieties of swede and turnip are also used with considerable success in certain areas.

Spongopora subterranea (Wallr.) Lagerh. has essentially the same life history as *Plasmodiophora brassicae*. There is the same doubt about a sexual fusion. In this case the resting spores produced from the plasmodium are formed in hollow spheres—the small, round spores forming a spongy network (Fig. 42). Sometimes there is more than one spore ball in a single infected cell. This fungus occurs on potato tubers, causing the disease known as Powdery Scab. It produces slight swellings early on, which suggest Wart Disease. Later, however, hollows are formed as the host cells disintegrate and the spore balls drop out. They form a loose, corky mass on the tuber surface.

PHYCOMYCETAE—OOMYCETES II

BLASTOCLADIALES

Blastocladiaceae—*Allomyces javanicus* Kniep grows in some soils. The coenocytic thallus is differentiated into a main axis (basal cell) and more slender, sympodial branches which are pseudo-septate (Fig. 43). It is attached to the substratum by branching rhizoids (Fig. 44). The whole thallus forms tufts up to several millimetres long.

The oval or barrel-shaped zoosporangia are terminal (Fig. 44a) or catenate (in chains). They are 60–80 μ long by 27–50 μ in diameter. The zoospores are ovoid, 11–12·5 by 8–10 μ in diameter and posteriorly-uniflagellate. They are discharged through one or more pores formed by the

Phycomycetae—Oomycetes II

deliquescence of prominent apical papillae. Thick-walled resting sporangia are borne similarly, on the same thallus (Fig. 44b). When they germinate meiosis takes place.

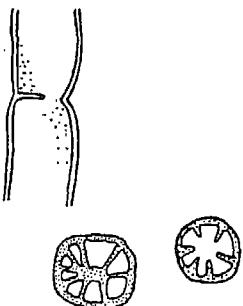


Fig. 43. *Blastocladiaceae*.
Pseudo-septate hyphae (after
Barrett, 1912)

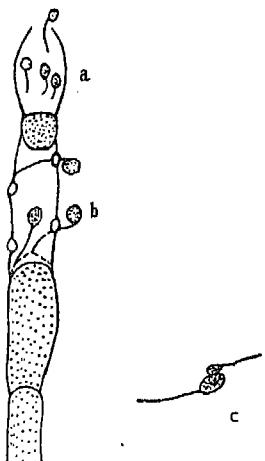


Fig. 45. *Allomyces javanicus*. Plant bearing gametangia. a Terminal antheridium; b subterminal oogonium; c lateral fusion of flagellated gametes which are unequal in size (after Sparrow, 1943)

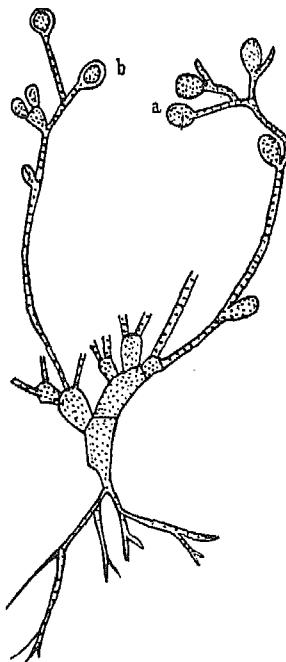


Fig. 44. *Allomyces javanicus*.
Rhizoidal, branching thallus bearing
a zoosporangium, b resting sporangia
(after Butler, 1923)

thallus in appearance. Sexual reproduction is anisogamous. The male gametangium (antheridium) is frequently terminal

Posteriorly - uniflagellate haploid "planonts" are produced. They give rise to sexual plants which resemble the asexual

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and single (Fig. 45a). It is cylindrical in shape with a narrow apex, about $35 \times 24 \mu$. If it occupies this position, it is subtended by the larger female gametangium (oogonium), roughly $50 \times 33 \mu$ (Fig. 45b). Both types of gametes are released. They are both posteriorly-uniflagellate. The male gamete is smaller and pigmented, the female larger and colourless. They fuse laterally (Fig. 45c). The zygote loses its flagella and gradually the two nuclei fuse. On germination the asexual thallus is reproduced.

MONOLEPHARIDALES

Monoblepharidaceae—*Monoblepharis polymorpha* Cornu is an aquatic saprophyte, growing on dead twigs and animal

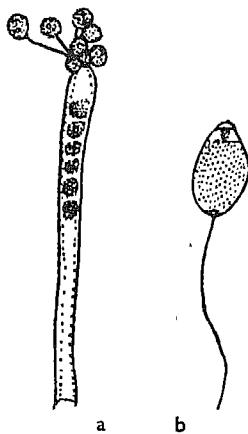


Fig. 46. *Monoblepharis polymorpha*,
a Terminal sporangium, containing
uniflagellate zoospores; b pos-
teriorly-flagellated zoospore (after
Sparrow, 1933)

remains, submerged in shallow water. The mycelium is filamentous and well developed. The hyphae are tapering, they bear terminally sporangia which are usually narrowly cylindrical, $130-234 \times 10.4-13 \mu$. They contain a small number of posteriorly uniflagellate zoospores, which are set free by dissolution of the apex of the sporangium (Fig. 46a). The zoospores are $10.4-13$ by $7.8-10.4 \mu$ (Fig. 46b). Both antheridia and oogonia are formed. The oogonia are terminal and pyriform, $20-28 \mu$ long by the same diameter tapering to $5-7 \mu$ at the apex. The oogonium contains one

Phycomycetae—Oomycetes II

oosphere. Antheridia are, typically, formed on the oogonium (epigynous) and are cylindrical (Fig. 47a). They are $10-35 \times 5-10 \mu$ and contain a number (5-7) of motile, uni-flagellate spermatozoids, $5.2 \times 2.6 \mu$. These are similar to the zoospores except for their smaller size. They are set free from an opening in the top of the antheridium. They may

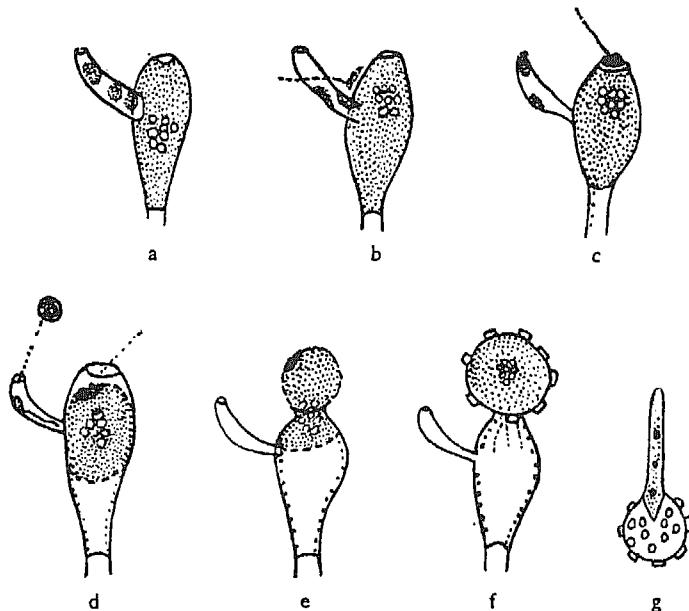


Fig. 47. *Monoblepharis polymorpha*. a Oogonium with epigynous antheridium; b male gamete approaching oogonium; c male gamete entering oogonium; d male gamete within oogonium; e emergence of fertilized egg; f development of thick-walled oospore; g germination of oospore (after Sparrow, 1933)

creep in an amoeboid manner or move freely (Fig. 47b). One penetrates the oogonium by means of an opening which has appeared at a well-defined apical papilla (Fig. 47c). The protoplasm of the antherozoid is engulfed by that of the oosphere and can be distinguished inside for some time (Fig. 47d, e). The fertilized egg emerges from the oogonium and develops into a non-motile, thick-walled oospore

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(Fig. 47e, f). The wall is rough. The oospore germinates by means of a germ tube (Fig. 47g).

SAPROLEGNIALES

Saprolegniaceae—If dead flies, meat or white of egg are added to pond water, *Saprolegnia monoica* Prings. or other species will grow saprophytically upon the materials. Pond water almost always contains resting oospores or zoospores of *Saprolegnia* spp. or *Achlya* spp. Hyphae grow all through the

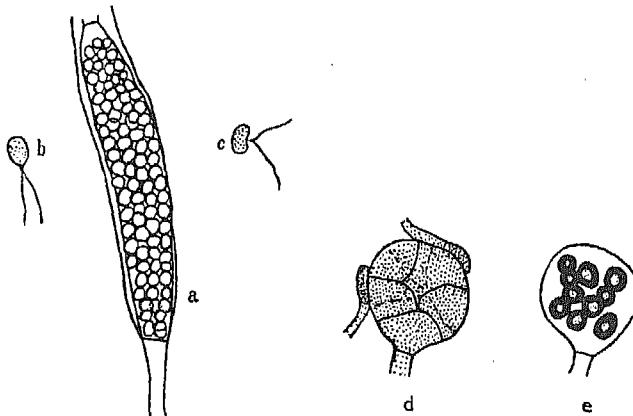


Fig. 48. *Saprolegnia monoica*. Zoosporangium and zoospores. a Zoospores with flagella attached; b terminally, c laterally in the two swimming stages; d oogonium containing oospheres and bearing two antheridial branches; e oogonium containing thick-walled oospores

organic matter and form a halo round it in the water. The hyphae are large, non-septate and branched, with dense protoplasm. Asexual reproduction takes place by means of club-shaped zoosporangia, produced at the ends of the hyphae. Proliferation of the zoosporangia commonly occurs. Many nuclei are cut off, each with a portion of the cytoplasm. Each ultimately gives a pear-shaped zoospore with two terminal flagella (Fig. 48a). They swim inside the sporangium. After some time they escape through a terminal pore (Fig. 48b), swim for a few minutes, come to rest, withdraw their flagella and develop a surrounding wall.

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About twenty-four hours later the protoplasm of the zoospore slips out from the wall. This time the two flagella are laterally attached (Fig. 48c). There are thus two swimming periods and two morphologically different swimming stages. This phenomenon is called diplanetism. The second type of zoospore also develops a wall but germinates by means of a germ tube. This type of asexual reproduction is abundant. If water is limited in amount, the accumulating products of growth of the fungus bring this phase to an end.

Asexual reproduction is followed by the appearance of antheridia and oogonia. The oogonium is terminal and spherical. It is multinucleate. The nuclei and protoplasm towards the centre disintegrate leaving a lining layer of nuclei. These nuclei divide once and an oosphere is produced round each. The antheridium appears as the end of a branch hypha. It is small, club-shaped and multinucleate. The nuclei divide at the same time as the oogonial nuclei. There may be several antheridia for each oogonium. The antheridium comes in contact with the oogonium and a simple or branched fertilization tube is produced, which pierces the oogonial wall (Fig. 48d). The conjugation tubes convey one male nucleus to each oosphere. Sexual fusions take place. Each oospore develops a thick, smooth wall (Fig. 48e). After a rest period, the oospore germinates by a tube which penetrates the common oogonial wall and gives rise outside either to a zoosporangium or to mycelium.

Although sexual fusion occurs in *Saprolegnia monoica*, this is by no means true of all members of the genus. In *S. ferax* there may be fewer antheridia than oogonia and fusion may not take place. In other species such as *S. monilifera*, oogonia only are formed.

Saprolegnia ferax is sometimes responsible for the death of salmon. It grows round the gills, interferes with their function and produces suffocation.

LAGENIDIALES

Lagenidiaceae—The genus *Lagenidium* contains species which grow as parasites on green algae. *L. rabenhorstii* Zopf.

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grows in the filaments of *Spirogyra*. Any one infection takes place by means of laterally-biflagellate, reniform zoospores and is confined to a single cell of the host (Fig. 49). The

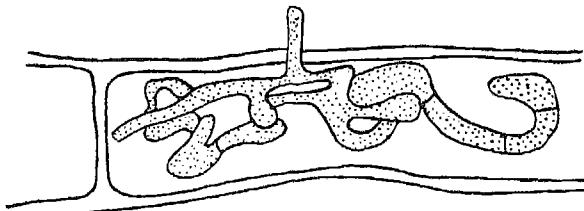


Fig. 49. *Lagenidium rabenhorstii*. Thallus within cell of *Spirogyra* (Smith, G. M., 1938, by courtesy of McGraw-Hill Book Co. Inc.)

zoospore germinates by a germ tube which penetrates the algal filament, giving rise, within, to one or more filaments which develop into the short, thick, simple or branched tubes of the mycelium. The filament becomes septate. Each portion is transformed into a sporangium, an antheridium or an oogonium. In asexual reproduction the

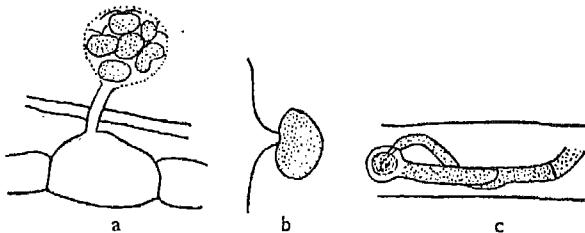


Fig. 50. *Lagenidium rabenhorstii*. a Zoospores in vesicle outside *Spirogyra* cell; b laterally-biflagellate zoospore; c old antheridium with conjugation tube joining it to oospore (Smith, G. M., 1938, by courtesy of McGraw-Hill Book Co. Inc.)

zoosporangium produces a fairly long tube which projects into the water outside. The partly-developed zoospores pass out into a vesicle at the end of the tube and there complete their development before being set free (Fig. 50a). They are $8.6 \times 6 \mu$ (Fig. 50b).

The sexual reproduction bears a curious resemblance to that of *Spirogyra* itself. It takes place by means of cylindrical

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antheridia and spherical oogonia $15-16 \mu$ in diameter. They are formed in adjacent segments and join by means of a conjugation tube (Fig. 50c). The spherical oospore formed as a result of fertilization is $10-20 \mu$ in diameter (Fig. 50c). It has been reported that the thick-walled oospore soon germinates with the production of a single, spherical biflagellate zoospore.

PERONOSPORALES

Pythiaceae—Species in the genus *Pythium* grow either as saprophytes or parasites on seedlings, roots and fruits of higher plants, on algae or on minute animals.

Pythium de baryanum Hesse occurs in soil as a saprophyte, but is often very destructive to young seedlings, attacking

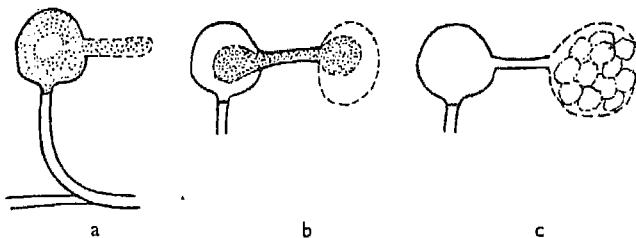


Fig. 51. *Pythium de baryanum*. a Sporangium producing tube at the end of which the spore-containing vesicle is developed; b sporangium with tube and developing vesicle; c sporangium with tube and vesicle containing the spores

them at soil level and causing the disease known as Damping Off. The effects of this attack can be well seen on an overcrowded pot of cress or mustard seedlings grown under very humid conditions. In this fungus the mycelium is well developed both within and outside the host tissues. The mycelium is intercellular, forming simple or branched haustoria which penetrate the host cells. It consists of slender, branched filaments, $3-4 \mu$ wide, which bear a small number of spherical to oval, multinucleate zoosporangia, cut off from the aseptate filaments by septa. The sporangia are either terminal or intercalary. They are $10-35 \mu$ in

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diameter. They are formed outside the host tissues. Each sporangium puts out a tube roughly equal in length to that of the sporangium. At the end of this a fragile vesicle is formed (Fig. 51). The multinucleate contents of the sporangium pass in through the tube, and within the vesicle give rise to as many reniform zoospores as there are nuclei. Each bears two laterally-attached flagella. Under drier conditions the zoosporangia may function as conidia. They germinate by means of a germ tube either soon after they are formed or after a rest of some months. In the former

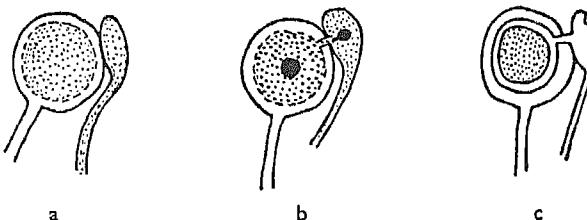


Fig. 52. *Pythium de baryanum*. a Oogonium with paragynous antheridium; b oogonium with paragynous antheridium and fertilization tube; c oospore

case germination may take place while the sporangia are still attached to the parent hyphae or after they become detached from them.

In *P. de baryanum* Hesse an oogonium develops terminally on a lateral branch and an antheridium is cut off at the end of a branch which may come from the stalk of the oogonium. The tips of these branches curve so that they are side by side and are applied to each other laterally. An antheridium formed in this position is said to be paragynous (Fig. 52a).

Oogonia are smooth, usually spherical, 15-25 μ in diameter. The young oogonium contains 10-15 nuclei, arranged round the periphery. They divide once; there is then a clear differentiation into central ooplasm and surrounding periplasm. One nucleus passes from the periphery to the centre and functions as the egg nucleus (Fig. 52b). The others degenerate.

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There are 1–6 antheridia for each oogonium. They arise as branches of the same hypha as the oogonium, or from different hyphae. The antheridium contains 2–6 nuclei which undergo one division simultaneously with the oogonial nuclei. All nuclei except one then degenerate. This nucleus, together with the greater part of the protoplasm, passes from the antheridium to the oogonium by means of a fertilization tube, which grows through the oogonial wall and periplasm and penetrates the egg (Fig. 52c). The two gametic nuclei fuse immediately and a thick wall forms round the uninucleate oospore. The oospore is smooth, 10–18 μ in diameter and does not fill the oogonium (Fig. 52c). On decay of the infected tissues, the oospores pass to the soil. They are able to overwinter there. Each either germinates directly into a hypha by means of a germ tube or produces a zoosporangium.

Infection of adult plant roots or of seedlings may be due to mycelium formed from germinating oospores, or to zoospores or to conidia. Zoosporangia and conidia are formed outside the infected tissues. Oospores are often formed inside the infected hypocotyl tissues of the cress seedlings and are only set free into the soil after the death of the host plant.

Damping Off may be caused by a number of different fungi. Whatever the organism causing it, the best method of control is by soil sterilization. This may be done by heat or by treatment with some fungicide, such as formaldehyde. These methods cannot easily be applied on a large scale in the field. In this case the seed is treated with an organomercuric or copper fungicide before sowing. Thus it is given a small area of fungus-free soil in which to develop and is enabled to pass through the critical seedling stages without becoming infected. Lighter sowings of seed, or any other factors which encourage good air and soil ventilation and reduce humidity, help to reduce the incidence of the disease.

Phytophthora is closely related to *Pythium* and separated from the latter genus only by the fact that the zoospores are formed inside the original sporangium and not in a

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vesicle. The sporangium may or may not produce an evanescent vesicle at the time that the mature zoospores escape. In *Phyt. infestans* (Mont) de Bary oogonia are sometimes formed in the absence of antheridia. The relative position occupied by these two organs is used as a taxonomic character. Thus, *Phyt. infestans* is grouped with those species in which the antheridia are amphigynous, i.e. during development the tip of the oogonial incept penetrates the tip of the antheridial branch and grows through it to emerge and form, on the other side, a round swelling which is the young oogonium (Fig. 53a).

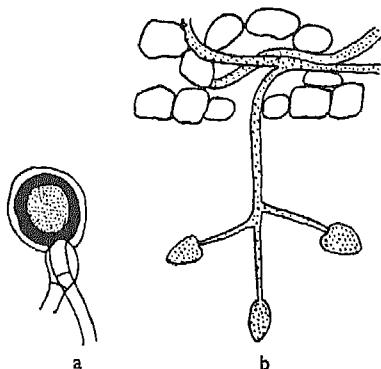


Fig. 53. *Phytophthora infestans*.
a Amphigynous antheridium beneath an oospore developed from a fertilized oogonium;
b branched sporangiophore emerging from stoma pore on lower surface of potato leaf

The genus contains species living part of their lives as saprophytic water moulds (Blackwell, Waterhouse and Thompson, 1941), yet capable of causing serious diseases of plants. The most widely known is *Phyt. infestans*, the organism responsible for Blight of potatoes. In Britain, the disease is commonly referred to as Potato Disease. Blight frequently assumes epiphytic proportions. In the field, in summer, it destroys the leaves and stems of growing plants. Attacked leaves early show brown areas. In muggy weather these spots quickly develop a halo of white, fragile sporangiophores. The mycelium is intercellular with branched haustoria in the cells and branched sporangiophores emerging through the stomata (Fig. 53b). The latter bear the lemon-shaped sporangia, $22-33 \times 16-24 \mu$, at the tips

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of their branches. Under humid conditions the spread of the fungus is very rapid and all the green parts of a potato crop may be destroyed or badly damaged in a matter of 10 days. This leads to great reduction in the crop produced and even those tubers which do develop may become infected by sporangia washed from the haulms into the soil. Such infected tubers contaminate healthy ones during handling at harvest and further heavy losses due to

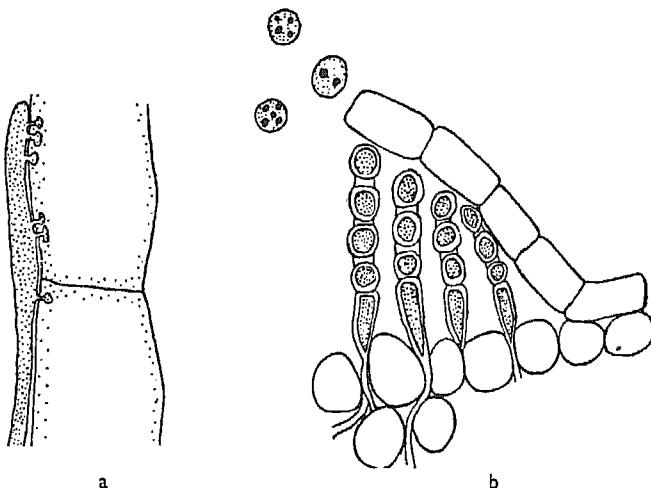


Fig. 54. *Cystopus candidus*. a Globose haustoria penetrating host cells from intercellular mycelium (after de Bary, 1887); b subepidermal conidial chains and multinucleate conidia

rotting in storage may result. Infected material has a characteristic, unpleasant, fishy smell.

The enormous economic importance of this disease, the catastrophic famines which it produced in Ireland, particularly in 1845, and the resulting mass emigrations from that country will not be further described here. The interested reader is referred to the historical account of the potato by Salaman (1949). Fortunately the disease can be adequately controlled by the routine application of fungicides to the growing crop. The best method, probably, is to apply copper sulphate in the form of the liquid spray

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known as Bordeaux Mixture. Breeding work has so far indicated that at least five "strains" of the fungus exist and that resistance in a potato variety to attack by one of these strains does not preclude susceptibility to the others, as five independently inherited dominant genes give resistance to two or more of the strains (Black, 1950).

Albuginaceae—*Cystopus candidus* (Pers. ex Chev.) Lév. is parasitic on members of the Cruciferae. It causes Blister Rust, White Rust or White Blister of plants such as cabbage and shepherd's purse. The disease causes mealy white pustules to appear on stems, leaves, flowers and fruits. The mycelium is intercellular with numerous, small, globose haustoria penetrating the host cells (Fig. 54a). The effect on the internal tissues is marked. The leaves, for example, become hypertrophied. All the mesophyll cells become twice or more their normal size and the distinction between spongy tissue and palisade is lost. A dense weft of hyphae is produced just below the epidermis. Short, erect, multi-nucleate portions of these hyphae grow towards the epidermis

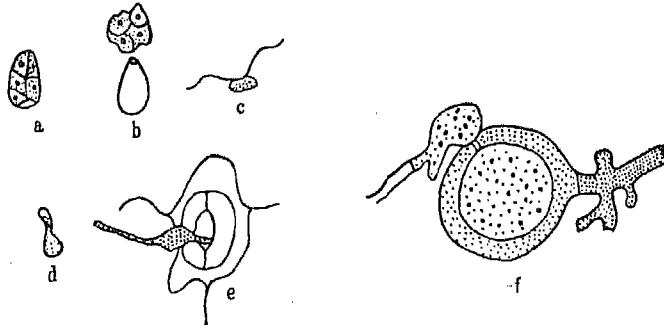


Fig. 55. *Cystopus candidus*. a, b, c Production of zoospores from the conidium; d germination of the zoospore; e penetration of a leaf by the germ tube from a spore; f paragynous antheridium and fertilization tube joining it to an oogonium within which an oospore has formed (after de Bary, 1887)

from the mat. The end of each portion swells slightly and is cut off by a cross wall as a sporangium (conidiosporangium) containing five to eight nuclei. The process

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may be repeated an indefinite number of times so that chains of sporangia, 12–18 μ in diameter, are formed. The mass of fungus tissue produced ruptures the epidermis. There is a short, sterile portion between adjacent sporangia in the chain (Fig. 54b). They separate from each other and are shed as conidia, being wind-borne to another host plant. Once the conidium has arrived there, the protoplast divides to form one reniform, biflagellate zoospore round each nucleus. The zoospores are then set free (Fig. 55a, b, c). After swarming they assume a spherical shape, secrete a surrounding wall and germinate by means of a hypha which penetrates the host tissues through a stoma pore (Fig. 55d, e). Sometimes the conidiosporangia germinate directly by a germ tube without the production of zoospores.

Spherical oogonia, 50–60 μ in diameter, and smaller, club-shaped antheridia are produced by hyphae which

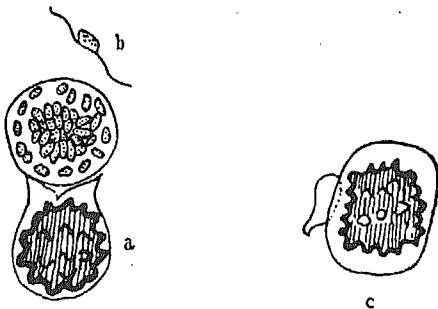


Fig. 56. *Cystopus candidus*. a Oospore with emergent vesicle containing developing zoospores; b biflagellate zoospore; c oospore with thick, irregular wall (after de Bary, 1887)

penetrate the deeper seated tissues of stem and petiole. The young oogonium is multinucleate and so is the egg when first marked off from the periplasm. All but one of the central nuclei disintegrate. There is one paragynous antheridium for each oogonium. A single fertilization tube is produced and penetrates the egg (Fig. 55f). The male gamete nucleus fuses immediately with the female nucleus. The oospore is 40–55 μ in diameter. It does not fill the

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oogonium. It soon surrounds itself with a thick wall (Fig. 56c). The fusion nucleus soon divides and many nuclei are formed. Oospores may rest overwinter. When germination takes place, up to 100 biflagellate zoospores come out into a thin vesicle (Fig. 56a). They are soon set free. They are exactly like the zoospores formed in the sporangia (Fig. 56b). They bring about the primary infection of new host plants.

Control is effected by the removal and destruction of all cruciferous waste, especially infected material which may contain oospores, and by the inclusion of as many non-cruciferous crops as possible in the rotation.

Peronosporaceae—There are a number of genera in this family. All comprise species which are parasitic on higher

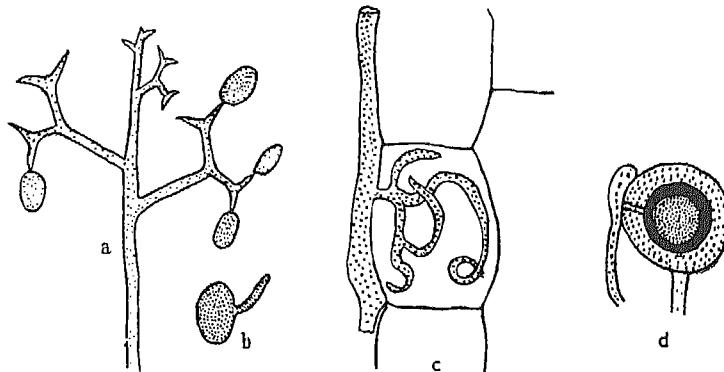


Fig. 57. *Peronospora parasitica*. a Dichotomously-branched conidiophore; b germinating conidium; c branched haustorium in cell of wallflower; d paragynous antheridium and oospore

plants. The mycelium in all cases is intercellular with haustoria penetrating the host cells. In *Peronospora* the haustoria are numerous and branched (Fig. 57c). The sporangiophores are sharply differentiated from the hyphae of the mycelium. They are branched and bear sporangia simultaneously at the tips of their branches. The branching is dichotomous and the branch ends are sharply pointed (Fig. 57a). This genus is regarded as containing the species furthest removed from the aquatic Phycomycetaceae. In

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P. parasitica (Fr.) Tul. the sporangia are broadly oval, $24-27 \times 15-20 \mu$. Typically, they function as conidia, germinating by means of a germ tube, as do the oospores (Fig. 57b). The latter are $30-40 \mu$ in diameter. Sexual reproduction is otherwise similar to that already described for *Cystopus* (Fig. 57d).

The fungi in this family cause the diseases known as the Downy Mildews. Thus *Peronospora parasitica* (Fr.) Tul. causes Downy Mildew of cabbage and many other cruciferous plants including wallflower, while *Plasmopara viticola* (Berk. and Curt.) Berl. and de Toni causes the serious Downy Mildew of the grape vine and *Bremia lactucae* Regel may be very destructive on lettuces under glass.

There are within many of the species in the Peronosporales sub-species which have been distinguished from each other, with the aid of infection experiments, by the host plant or plants on which they occur. Sometimes these distinctions are supported by small differences in sporangial measurements. Thus, *Peronospora parasitica* was broken up by G  umann and Dodge (1928) into some 20 species, some of which occur only on a single species of host plant. In *Phytophthora infestans* there are within the species strains which can be distinguished by the differing reaction to them of the host plant. Plant breeding work designed to produce commercial potato varieties resistant to blight has shown that there are at least five strains present, of which one is much the commonest.

The fertilization of the egg *in situ* by a male gamete conveyed to it passively through a fertilization tube means that water is no longer necessary in order to allow the fungi in this group to complete sexual reproduction. The stages in the transformation of the asexual sporangium from the zoosporangium, setting free swimming spores, to the air-borne conidium, have been outlined by reference to examples in the genera *Pythium*, *Phytophthora*, *Cystopus* and *Peronospora*. This change completes the freeing of the fungi concerned from dependence on the presence of free, liquid water. This is, too, an example of a change beneficial

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to the organism concerned yet consisting of a degeneration as opposed to a specialization process, in that the whole of the sporangium is now performing the work previously carried out by a part.

These two changes have combined to render the higher members of the Peronosporales independent of an aquatic environment and have opened up the possibility of their growth on the subaerial portions of land plants occupying typical dry land habitats.

8

PHYCOMYCETAE—ZYGOMYCETES

MUCORALES

THIS ORDER is divided into seven families, on account of sporangial characters, by Fitzpatrick (1930). It includes the Black or Pin Moulds, typically species of *Rhizopus* and *Mucor*.

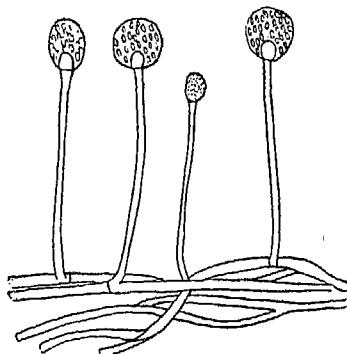


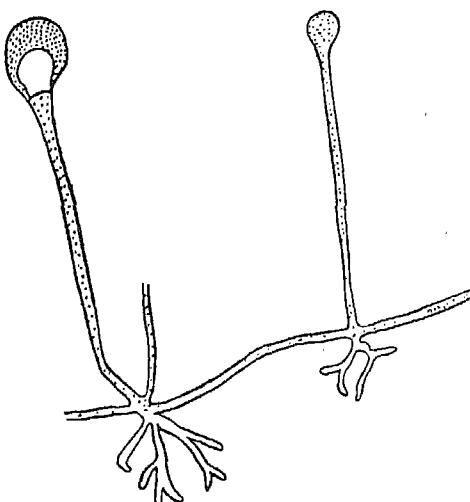
Fig. 58. *Mucor mucedo.*
Sporangia

Many species are terrestrial saprophytes on plant and animal remains. They are most numerous in cultivated soils (Campbell, 1938). Some are found commonly as moulds of foodstuffs, e.g. *Rhizopus nigricans* Ehrenberg on bread, and

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others are used industrially in fermentation processes and starch hydrolysis (Smith, 1946). A few are parasitic on other members of the same order, e.g. *Chaetocladium brefeldii* van Tieghem and Le Monnier on *Mucor* spp., or on Basidiomycetae, e.g. *Spinellus macrocarpus* Corda on *Mycena paelonga* Peck or *Sporodinia grandis* Link on old decaying mushrooms. More rarely they may be associated with diseases of man. *Mucor pusillus* Lindt. may cause mycosis of internal organs.

Fig. 59. *Rhizopus nigricans*. Sporangia with columellae, associated with "rooting hyphae"



There is a well-developed, freely-branching mycelium. The vegetative hyphae are non-septate. They bear the sporangia which contain the non-flagellate, non-motile aplanospores.

In addition to reproducing asexually by means of sporangia, the fungi reproduce sexually by means of multinucleate gametangia. These are, typically, identical in shape, size and behaviour, though sometimes this isogamy is departed from.

In the Mucoraceae common species include *Mucor mucedo* Lin., which occurs on dung. It produces its sporangia more or less irregularly over the whole mycelium (Fig. 58). In this it differs from *Rhizopus nigricans* Ehr. which has its sporangiophores in groups associated with special smaller,

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pointed hyphae, termed stolons, rooting hyphae or rhizoids (Fig. 59). The sporangia are raised on their stalks well above the general level of the mycelium. During maturation of the sporangium, the end of a branch swells, nuclei go in and the protoplasm, which is at first uniform, becomes separable into dark, outer, and clear, inner regions. The peripheral layer is cleaved into uninucleate masses which produce the spores, while the central part is separated off by a concave wall as the sterile columella (Figs. 59, 20). The spores are, of course, non-motile and are wind distributed.

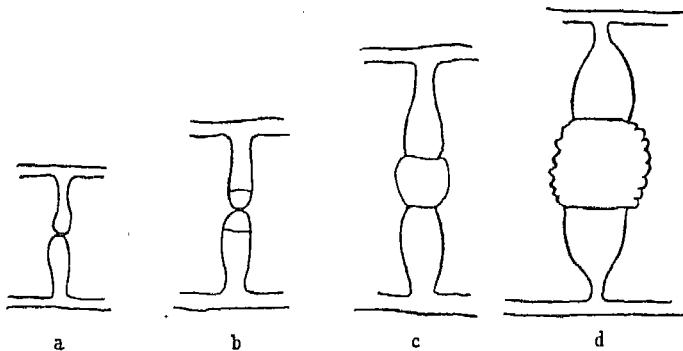


Fig. 60. *Mucor mucedo*. Stages in the formation of the coenogzygote. a fusion of branches; b differentiation of gametangia; c fusion of gametangia; d development of thick-walled coenogzygote

In *Mucor mucedo* monospore cultures show that for the formation of the perfect stage—the sexual zygospores—it is necessary that the union of two different mycelia should take place. This is an example of the phenomenon of heterothallism. It occurs in all groups of fungi. The two mycelia are morphologically indistinguishable yet differ in their "attributes" or "potentialities" and are designated the plus and the minus mycelium. Their branches may join terminally or laterally. As a result of the stimulus of contact, the extreme tip of each branch is differentiated into a multinucleate gametangium (coenogamete), which is cut off by a cross wall from a suspensor immediately below (Fig. 60a, b). The two gametangia are identical. The wall

Phycomycetae—Zygomycetes

between dissolves and fusion of a number of pairs of nuclei takes place. As a result a coenozygote is produced (Fig. 60c, d). The fusion nuclei divide by a reduction division. The zygospore forms inside this cell. Its wall is composed of a number of layers. The outermost is roughened and is the wall of the original cell. After a rest period of 5-9 months the zygospore germinates by the immediate production of a sporangium. Morphologically this is similar to the ordinary sporangia. In *M. mucero*, it contains only one kind of spore. Spores from this type of sporangium on germination give all plus or all minus mycelia.

The difference between strains is usually accepted as being one of sex. Differentiation of the strains is said to take place

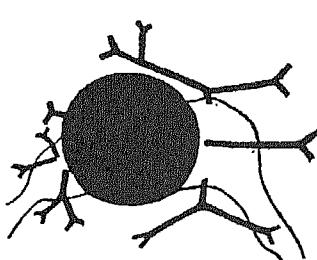


Fig. 61. *Phycomyces nitens.*
Zygospore

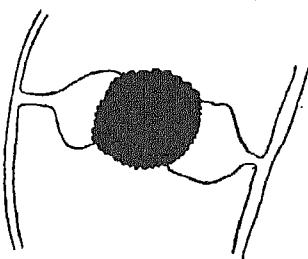


Fig. 62. *Sporodinia grandis.*
Zygospore

during the nuclear division immediately after the fusion of the zygote nuclei, i.e. prior to the dormant stage of the zygospore. As the spores in the germ sporangium are all plus or all minus then it follows that the nuclei which they contain must have originated from a single nucleus, i.e. that the germ sporangium is originally uninucleate. The condition with regard to the spores varies in different species throughout the order.

In some other heterothallic species one type of mycelium grows a little more vigorously than the other. Where this is so, it is usual to regard it as belonging to the plus strain.

Phycomyces nitens (Agardh) Kunze is a heterothallic species growing on fat-containing material. It is like a large *Mucor*

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and is 4–6 inches high. The zygospores have spine-like processes growing from the suspensors (Fig. 61).

Segregation of sex occurs preceding the formation of sporangiospores in the germ sporangium. The sporangium contains both plus and minus spores. Segregation is only partial, however, and there are a number of spores which are both plus and minus. These last on germination give rise to homothallic mycelia. This homothallism is unstable. The sporangia produced on such homothallic mycelia contain plus, minus and homothallic spores.

Sporodinia grandis Link is a saprophytic species growing on decaying fungi. It shows sporangia of an advanced type produced on repeatedly-branched sporangiophores, with

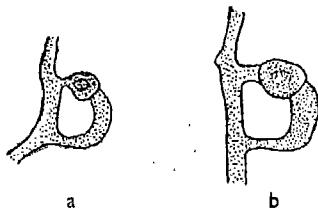


Fig. 63. *Zygorhynchus moelleri*.
a Fusion of unequal gametangia;
b zygospore with unequal suspensors
(after Green, 1927)

reduction in the amount of sporogenous tissue and therefore of spores. The species is homothallic. The fusing gametangia form on branches of the same mycelium, which are raised above the general hyphal level. When the fusion of the coenogametes takes place one is slightly larger than the other (Fig. 62).

Zygorhynchus moelleri Vuillemin shows the difference between gametangia much more pronouncedly. One gametangium is much larger than the other and even its suspensor is more obviously swollen (Fig. 63). This additional evidence makes it seem probable that the differences between the plus and minus strains are indeed sexual in character and many workers regard the larger gametangium as being the female structure and the smaller as the male.

Chaetocladiaceae—In *Chaetocladium brefeldii* van Tieghem and le Monnier the tendency for reduction in the spores within the sporangium already noted in *Sporodinia grandis* is

Phycomycetae—Zygomycetes

carried to the extreme and a single-spored sporangium is produced (Fig. 64a). This may be termed a conidium. On germination it is seen to be a two-walled structure, the sporangium wall remaining behind empty when the spore is set free (Fig. 64b, c).

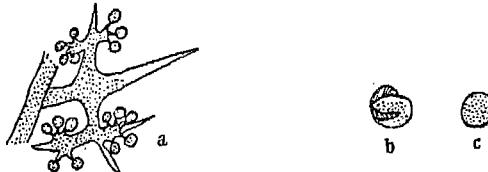


Fig. 64. *Chaetocladium brefeldii*, a Production of single-spored sporangia; b, c germination of conidium (adapted from Brefeld, 1872)

Endogonaceae is typified by species of *Endogone* which are subterranean saprophytes. Both sporangia and zygospores tend to be joined in groups to form fructifications. The groups

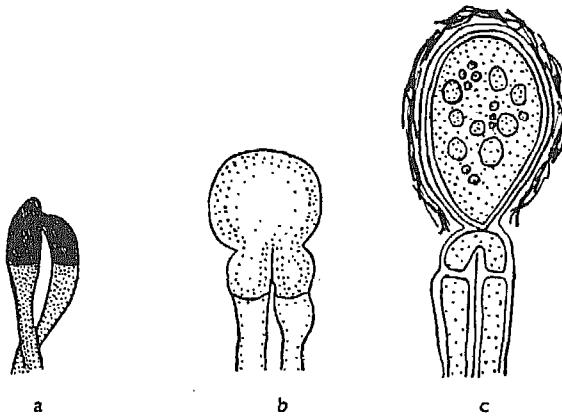


Fig. 65. *Endogone*. a Unequal gametangia; b sac developing from the larger of the two gametangia; c zygospore (adapted from Thaxter, 1922)

are usually separate. They are protected by interwoven masses of vegetative hyphae. The gametangia are unequal in size (Fig. 65a). In *E. lactiflu* Berk. each gametangium becomes uninucleate when mature. They fuse laterally and a sac grows out from the larger of the two (Fig. 65b). This

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subsequently develops into the zygospore (Fig. 65c). Both nuclei pass in; but their fusion is delayed till the germination of the zygospore.

ENTOMOPHTHORALES

All the five genera belonging to this order are placed in one family, Entomophthoraceae. Most of the species are parasitic on insects (entomogenous). *Empusa muscae* Cohn occurs quite commonly on house flies in autumn. Insects are seen, after death, anchored to window panes, etc., by strands of the mycelium. They appear surrounded by a halo of hyphae and conidia. The mycelium in this order is much reduced as compared with the Mucorales. There is a general tendency for it to be septate. The septa divide the hyphae into plurinucleate or even, in *Basidiobolus*, uninucleate segments. In some genera these segments separate forming hyphal bodies. The latter increase rapidly in number by fission and budding. Asexual reproduction is by sporangia which are shot off singly from the apex of a rather club-shaped sporangiophore. The sporangia show all stages from the multinucleate sporangia of *Basidiobolus*, which still develop sporangiospores, to the uninucleate sporangia germinating by means of a germ tube, which occur in many species of *Entomophthora* and are homologous with the reduced sporangia occurring in *Chaetocladium* among the Mucorales.

PHYCOMYCETAE RELATIONSHIPS

IN THE case of the Phycomycetae it is worth while to deal fairly fully with the different views expressed on their origin and interrelationships. Such rather extended treatment brings out the fact that various authorities interpret the available evidence in different ways. The same is true of

Phycomycetae Relationships

every similar mycological problem. This one example should drive the point home.

Pringsheim (1858) suggested a close relationship between living groups of fungi and algae, linking the genera of the Saprolegniales with the siphonaceous green algae. These views gained wide acceptance. Sachs (1872) linked all the groups of fungi with algal groups—the Phycomycetae with green algae and the Ascomycetae and Basidiomycetae with red algae. Clements and Shear (1931) relate all the fungi in the Phycomycetae to one of four orders of green algae. They place in the Protococcales those fungi in which the mycelium is lacking or scanty, which propagate by amoeboid cells and spores or by sporangia and zoospores, and in which sex cells are rare, e.g. Plasmodiophoraceae, Synchytriaceae, are referred to the Protococcales. Filamentous forms reproducing by unlike gametes produced in antheridia and oogonia, as in Peronosporaceae, are assigned to the Vaucheriales. The Blastocladiales and Monoblepharidales are described as “typically multicellular forms” and assigned to the Confervales. Lastly, the Zygomycetae are linked with the order Spirogyrales. This classification is based on the idea that all phycomycetous fungi have been derived from the green algae by loss of chlorophyll following on the adoption of a saprophytic or parasitic mode of life, i.e. that all are degenerate green algae.

To accept that this close linkage exists between extant algae and fungi is probably too extreme an attitude to adopt. Yet Gaumann and Dodge (1928) considered that all true fungi (Phycomycetae, Ascomycetae and Basidiomycetae) were derived in monophyletic line from the Chlorophyceae, while the forms which they included as Myxomycetae and Archimycetes (Synchytriaceae and Plasmodiophoraceae of this book) were credited with a separate flagellate ancestry. This belief in an algal ancestry for all true fungi has many adherents. Great importance is attached to the similarity of the mycelium of the Monoblepharidales and Saprolegniales to the non-septate, coenocytic filaments of forms such as *Vaucheria* among the Siphonophyceae.

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Growth is apical and the broadish filaments contain numerous nuclei embedded in granular cytoplasm. Streaming of the protoplasm is to be seen. The zoospores of most Siphonophyceae (but not *Vaucheria*) are pear-shaped and bear two apical flagella so that they resemble closely the primary zoospores of the Saprolegniales. The typical iodine reaction for cellulose is only given by the cell walls in Monoblepharidales and *Vaucheria* after treatment with strong KOH. These among other features are used to support the theory of an algal relationship for the Phycomycetae. This view is further and strongly supported by the results of Mez's (1929) "sero-diagnostic" studies. Similar methods are being applied to the questions of relationships among other plant groups. Their application has so far been sporadic and the acceptance of the validity of the interpretation placed on the results obtained has been limited. Should this method come to be more generally accepted and applied, then the whole problem of the interrelationships in the Thallophyta will have to be reconsidered.

Smith (1938) adopted the views of Fischer (1892) and others that all fungi are derived monophyletically from the protozoa. He placed the Chytridiales "at the bottom of the phycomycetan series" and from them derived two series, one uniflagellate (Blastocladiales, Monoblepharidales), the other biflagellate (Lagenidiales, Saprolegniales, etc.). In this view the chytrids such as members of the Cladochytridaceae are regarded as primitive, leading to the other groups of the Phycomycetae. In the former, older view they are regarded as "retrogressive" from the higher Phycomycetae. As a preliminary to a detailed study of this problem it is essential to make sure which fungi are included in the Chytridiales. Different authorities employ this ordinal name in widely differing senses. The main facts used as arguments in support of the view that the chytrids are primitive are the sexual reproduction by motile isogametes and the simple structure of the plant body. It is also held that the flagellated zoospores and gametes of the chytrids bear a much closer resemblance to protozoa than they do to the zoospores and

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motile gametes of the green algae. Motile, uniflagellate swimmers occur in most chytrids. They are common among protozoa and unknown among green algae. This obvious character is linked with less easily explained features of the metabolism of the protoplast.

Sparrow (1943) touches briefly on the two views of this problem dealt with above before giving a somewhat more expanded statement of the views of Scherffel. He accepts Scherffel's general conclusions and his view of the relationships among the Phycomycetae may be summarized as follows. There are within the Phycomycetae two series, each derived from different "monad" ancestors: on the one hand uniflagellate, on the other biflagellate. The first series includes the Chytridiales (the anomalous position of Chladochytriaceae should be noted) and Blastocladiales with the Monoblepharidales as a terminal group. The second series includes Plasmodiophorales and is divided into two subseries, the one containing Saprolegniales, the other Peronosporales. The main characters distinguishing the two series are re-stated below.

In the chytrid series the zoospore is posteriorly uniflagellate, the protoplasm is homogeneous with no or few granules and one conspicuous oil globule. The spores are monoplanetic and they frequently have a short rest period as soon as they come out of the sporangium. They often exhibit erratic movement showing a hopping motion alternating with periods of amoeboid creeping, accompanied by changes of shape. The resting spores are formed from a whole cell by direct transformation and do not as a rule rest within the containing wall of a mother cell.

In the Saprolegniales-Peronosporales series the zoospores are biflagellate, the secondary zoospore bearing a shallow longitudinal groove from which arise two usually nearly equal but oppositely directed flagella. The cytoplasm is granular and there is no single globule contained in it. The spores show more or less well-developed diplanetism and the great majority lack the power of amoeboid movement. The resting spore is borne inside a containing wall.

ASCOMYCETAE—GENERAL AND CLASSIFICATION

ALL SPECIES in this class have a reproductive structure in the form of a sporangium, the ascus, containing typically eight spores. These spores are formed in a manner unique to the class namely by free cell formation. Round each of the nuclei in the ascus is cut off a portion of cytoplasm which

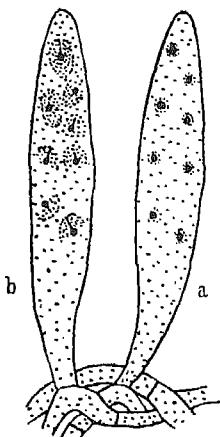


Fig. 66. *Pseudopeziza medicaginis*. Asci containing: a 8 ascospore nuclei; b 8 developing ascospores

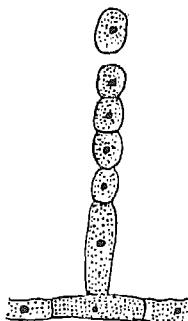


Fig. 67. *Erysiphe*. Unbranched conidial chain

is separated from the rest of the cytoplasm in the ascus by a plasma membrane (Fig. 66a, b). The cytoplasm not included within the ascospores is called the epiplasm. It contains materials such as glycogen and is used as food by the developing spores. Each spore is next surrounded by a spore wall (Fig. 26). Accompanying this process there is a gradual reduction of the epiplasm.

There is a relatively small number of species, such as the

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yeasts (Saccharomycetaceae), in which no mycelium is developed. All other Ascomycetac develop a septate mycelium. The mycelium may produce one or more types of non-flagellate, asexual spores. These may be borne on the terminal portions of hyphae on any part of the mycelium, as in the Powdery Mildews (Erysiphaceae), where chains of spores are cut off in acropetalous succession. Such spores are termed conidia (Fig. 67). Resistant sclerotia (Fig. 68) and chlamydospores (Figs. 20, 24) too, are often formed in the Ascomycetae. Where sex organs are recognizable, they are formed at the apices of the hyphae, usually on short, lateral



Fig. 68. *Botryotinia*.
Sclerotia

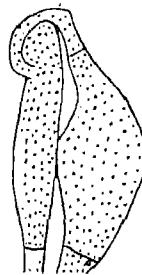


Fig. 69. *Pyronema confluens*.
Antheridium and ascogonium with
trichogyne (after Gwynne Vaughan
and Barnes, 1937)

branches. Mycelia may be homothallic, bearing both antheridia and ascogonia (oogonia) (Fig. 69); or they may be heterothallic, these organs being borne on different mycelia. In addition, the mycelia of homothallic forms may exhibit self-sterility.

The variation in the appearance of both antheridium and ascogonium, the steps leading to their fusion and the subsequent development of the ascus will be described under a number of species. The importance of these phenomena will be discussed in Chapter 14.

The organs are identical in a few genera only, such as *Eremascus*. In others, typified by *Pyronema*, they differ markedly in appearance. There is a tendency for the antheridium to fail to function and even to degenerate. It finally disappears in what are regarded as more highly evolved forms, for example *Neurospora tetrasperma*. Associated with this change, the ascogonium becomes less and less

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easily distinguished from an ordinary vegetative hypha. In some species in which antheridia are absent, they have been shown to be replaced by spore-like bodies named spermatia, which resemble minute conidia. Sometimes these are formed remote from the ascogonia and often in flask-shaped cavities named spermogonia, opening superficially on the tissue which bears them (Fig. 70c). The spermatia become detached from the spermogonia and are carried in various ways over the surface of the thallus to the vicinity of the

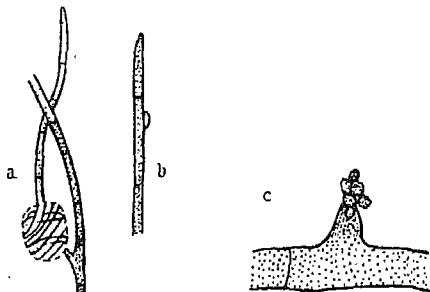


Fig. 70. *Pleuroge anserina*.
a Ascogonium with trichogyne; b trichogyne with fused spermatium;
c spermogonium (adapted from Ames,
1934)

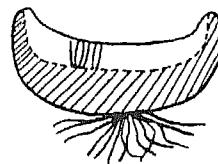


Fig. 71. Diagrammatic drawing of an open, cup-like apothecium showing two ascia and paraphyses

ascogonia. In fungi of this type the distal end of the ascogonium is drawn out into a thread-like, often multi-cellular trichogyne which projects above the surface of the fungus and, or, host tissues (Fig. 70a). The spermatium fuses with, and its contents pass into, the trichogyne. Fusion of the spermatial nucleus with that of a female gamete in the ascogonium has not been fully proved but, presumably, the spermatium acts as an antheridium and contains a functional male nucleus (Fig. 70b).

There is a tendency throughout the class towards the development of pseudo-parenchyma. This becomes very marked in what are regarded as the higher orders. There the pseudo-parenchyma assumes characteristic shape and size and its development is connected with the reproductive

Ascomycetae—General and Classification

processes. The fructifications thus formed may produce conidia or asci giving rise to ascospores. The conidiophores bearing the conidia or the asci producing the ascospores are borne in regular rows upon a mass of pseudo-parenchyma. Either conidiophores or asci may be interspersed with sterile hyphae called paraphyses. The layer of asci and paraphyses is called the hymenium.

In a great many species typified by those in the genus *Peziza* the hymenial layer is freely exposed as the inner surface of a shallow cup when the asci are ripe. This type of fructification is called an apothecium (Fig. 71). The ascospores are set free from the asci on to the surface of the

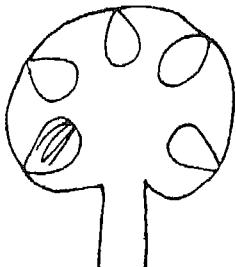


Fig. 72. Diagrammatic drawing of a stroma with embedded, flask-like perithecia, one showing an ascus and paraphyses

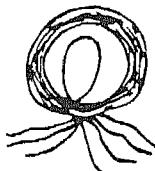


Fig. 73. Diagrammatic drawing of a closed fructification or cleistothecium containing one ascus

hymenial layer. In many other species the hymenium remains enclosed within the pseudo-parenchyma even at maturity. The ascospores, once released from the asci, escape to the outside through a small hole, the ostiole, at the end of a neck. The length of the neck varies according to the depth at which the hymenial layer is situated within the pseudo-parenchymatous mass. Such enclosed fructifications are called perithecia (Fig. 72). They occur in *Claviceps*. The same term is also often applied to the enclosed fructifications of the Powdery Mildews (Erysiphaceae), etc. Here, however, there is no ostiole, the ascospores escaping from the asci after the breakdown of the retaining wall of the fructification (Fig. 73). Such structures are more properly called cleistothecia.

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The classifications of the Ascomycetae in general use are based on the three divisions: Plectomycetes, containing all those species in which neither apothecia nor perithecia are formed; Discomycetes, containing those forming apothecia; and Pyrenomycetes containing those forming perithecia. This does divide the species into three fairly distinct sub-classes and for the mechanical running down of specimens has obvious advantages; but the Plectomycetes at least is a very artificial group. A much truer idea of the developmental trends in the Ascomycetae can be obtained by considering first examples of those species in which the ascus develops directly from the zygote and in which the asci are borne separately on the mycelium without any development of protecting sterile hyphae. From such a starting point the gradual separation of ascus formation from zygote formation can be traced, followed by the development of increasingly profuse pseudo-parenchyma, giving more protection to the asci and followed by the suppression of the formation of the sexual organs.

In each sub-class there is a number of orders. Only a selection of these is referred to below.

Plectomycetes—The asci arise either directly on the ordinary mycelium or on special parts of it. They are not united into a fertile layer or hymenium enclosed in or borne on a complex fructification.

Plectascales: Asci occur irregularly.

Eurotiales: Asci are formed in cleistothecia, opening irregularly.

Conidia are produced in chains, forming tufts on definite conidiophores.

Erysiphales: Asci occur in well-defined cleistothecia which are borne on a superficial mycelium.

Exoascales: Asci are exposed when mature. No fructification is formed.

Ascomycetae—General and Classification

Pyrenomycetes—Ascii are formed on a hymenium which lines the inside of a hollow, closed fructification, the peritheium. The fructification is often flask-shaped and with a mouth or neck through which the ascospores are set free at maturity. In each of the two orders a series may be traced ranging from forms in which the perithecia occur freely on the mycelium, through those in which they are partially embedded in a stroma, to those with perithecia entirely embedded in a stroma which is well-developed and, frequently, stalked. Conidial forms are common.

Hypocreales: The perithecia are fleshy and often brightly coloured.

Sphaeriales: The perithecia are brittle or leathery and dark in colour.

Discomycetes—The ascii are formed in a hymenium exposed at maturity on the surface of an apothecium. The apothecium is frequently cup-shaped; except in the morels in which it takes the form of a stalked structure with a convoluted head, and, in the truffles, among which it is an underground structure with the hymenium lining internal chambers or passages.

Phacidiales: The hymenium is sunk in the substratum and covered by it until maturity.

Pezizales: The hymenium is exposed as the inner surface of a cup, or on the convolutions of a head.

Tuberales: These are subterranean forms in which the hymenium lines internal chambers or passages within the fructification.

ASCOMYCETAE—PLECTOMYCETES

PLECTASCALES

THE SPECIES *Eremascus fertilis* Stoppel. belongs to the family Endomycetaceae. It was discovered growing as a mould on currant and apple jelly. It has a branched, transversely-septate mycelium. The cells towards the tips of the hyphae may be multinucleate, those in the older parts of the mycelium are uninucleate. Small outgrowths are developed in pairs one on either side of the transverse wall separating

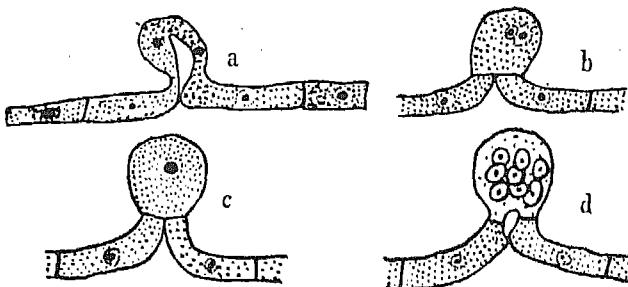


Fig. 74. *Eremascus fertilis*. Adjacent uninucleate cells a forming gametangia and fusing, b association of their nuclei, c followed by fusion, and d the division of the fusion nucleus to form 8 ascospores (Smith, G. M., 1938, by courtesy of McGraw-Hill Book Co. Inc.)

two adjacent uninucleate cells. These are the equal gametangia (Fig. 74a). The nucleus in each gametangium divides and one of each resulting pair of nuclei migrates to its tip to act as a gamete nucleus. The tips of the outgrowths unite, the walls disappearing at the point of contact. The gametes pass into the developing zygote, where fusion takes place (Fig. 74b, c). Later a transverse wall is formed cutting off the enlarging zygote. The zygote develops directly into a naked ascus. Its nucleus divides three times to form

Ascomycetae—Plectomycetes

eight nuclei. Free cell formation then takes place dividing the protoplast into eight uninucleate ascospores (Fig. 74d). There is some epiplasm left over. The spores are set free by disintegration of the ascus walls. In this species asci sometimes develop parthenogenetically from each of the protuberances without fusion taking place between the latter.

The genus *Eremascus* is an example of one in which the cytology of species has recently been critically re-examined, yet in which the very small size of the nuclei has made it impossible to analyse the details of nuclear division (Harrold, 1950).

The family Saccharomycetaceae comprises the yeasts, which are regarded as being forms reduced from types similar to the preceding. The septate mycelium has broken up into separate cells which increase in number by vegetative budding in *Saccharomyces* (Fig. 75), or by fission in



Fig. 75. *Saccharomyces*.
Cell division in a budding
yeast



Fig. 76. *Schizosaccharo-*
mycetes. Cell division in a
fission yeast

Schizosaccharomyces (Fig. 76). In the former genus the parent cell buds off a daughter cell which is smaller than itself at the moment of separation. In the latter, the parent cell is split into two equal parts by a transverse wall. In each case nuclear division precedes the separation of the two parts both of which thus remain uninucleate.

Most of the yeasts grow as saprophytes in sugary liquids exuded from plants, on the surface of fruits, the nectaries of flowers, etc. They are frequently present in the air. Some are parasitic on animals.

Most saprophytic yeasts break down sugars to carbon dioxide and ethyl alcohol when grown under anaerobic conditions. The production of carbon dioxide is made use of in baking and that of alcohol in a wide range of industrial processes. Certain species of yeast are much better than others in effecting these processes. The existence of many

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wild yeasts which may be present as contaminants makes it necessary to take elaborate precautions to ensure that only the desired commercial "strain" is allowed to bring about the fermentation. The inadvertent use of wild types may introduce undesirable flavours and odours, and otherwise interfere with the uniformity of the products obtained.

The habit of growth of the yeasts may be due in part to their environment, for species of *Mucor* or *Rhizopus* tend to grow in the same way, as separate cells, and to reproduce by budding when they are grown under the surface of liquids.

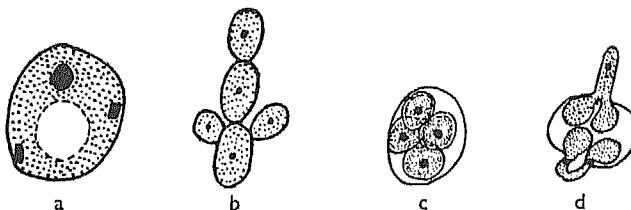


Fig. 77. *Saccharomyces*. a Cell showing nucleus, vacuole and cytoplasmic granules; b cells forming branched chains; c formation of 4 ascospores; d pairs of ascospores conjugating to form dumbbell-shaped structure (c and d Smith, G. M., 1938, by courtesy of McGraw-Hill Book Co. Inc.)

Saccharomyces cerevisiae Hansen is one of the bread yeasts. Its cells are more or less oval and measure about 10μ in length. Each contains a single small nucleus and a number of rounded or angular granules of reserve food material. The rounded granules are either glycogen or fats and the angular bodies are protein in nature (Fig. 77a). When the bud is forming, the nucleus divides and one of the daughter nuclei passes into the bud. The constriction between the parent cell and the bud is then closed. Careful examination has shown that each yeast cell may bear two small scars—one which marks the point of its previous attachment to its own parent and one which marks the former position of the bud to which it has given rise. The bud may not separate immediately and, when the budding is repeated, the cells may remain joined together in unbranched or branched chains (Fig. 77b). If the cells are removed from the liquid

Ascomycetae—Plectomycetes

medium and placed under damp conditions, four ascospores are formed inside each cell (Fig. 77c). In *S. ludwigii* Hansen it has been shown that when these ascospores germinate conjugation takes place (Fig. 77d). The cell resulting from the fusion of the two germinating ascospores may divide repeatedly. It seems very probable that the vegetative cells here are diploid and that meiosis takes place during ascospore formation.

In *Schizosaccharomyces octosporus* Beyerinck, among the fission yeasts, conjugation of pairs of cells precedes ascospore formation. Each of the cells sends out a short protuberance. These unite to form a conjugation tube into which the two nuclei migrate and fuse. The resulting zygote is often dumbbell-shaped. The fusion nucleus divides three times and round the eight nuclei thus formed in the ascus eight ascospores are produced. The germinating ascospores develop into ordinary vegetative cells. Here, apparently, the ascospores and vegetative cells are haploid and the zygote nucleus only is diploid.

EUROTIALES

In this order and in those dealt with subsequently the asci are not borne separately but arise associated in groups. The groups are protected by a common wall of sterile hyphae known as the peridium and the definite fructification thus formed is called an ascocarp. In the Eurotiales the asci lie irregularly distributed within the ascocarp. The wall does not open at maturity. This type of fructification is called a cleistothecium or cleistocarp (Fig. 73).

In the family Eurotiaceae asci and ascospores are produced by some of the species only. Some of the species are homothallic and others are heterothallic, forming asci only when two mycelia of different strain are allowed to grow together. Species of *Eurotium* are homothallic, as far as is known (Fig. 78). Two types of conidial stage occur commonly. These may persist as imperfect fungi without ever forming perfect stages. They are referred to the genera *Penicillium* and *Aspergillus*. Some species of *Aspergillus* are known to be

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the conidial stages of species of *Eurotium*. Both types of imperfect stage are very well known as mould fungi. Intensive studies of each have been published: of the former by Thom (1930), of the latter by Thom and Church (1926) and Thom and Raper (1945).

Penicillium roquefortii Thom has long been used in the ripening of cheeses such as Roquefort and Gorgonzola. The majority of species are saprophytes on decaying plant and animal remains. A few are parasites on living, stored plant materials, e.g. *Penicillium cyclopium* Westling on *Scilla* bulbs (Macfarlane, 1939) and *P. digitatum* Saccardo causing a dry rot of fruit. A form closely allied to *P. rugulosum* Thom is

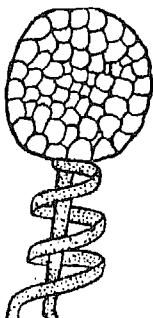


Fig. 78. *Eurotium*. Cleistothecium formed after fusion of antheridial and ascogonial hyphae

parasitic on *Aspergillus niger* van Teighem in culture. The genus has sprung into great prominence since the 1939-45 war as some of its species, notably *P. notatum* Westling, are sources of penicillin, the first of the antibiotic substances to be produced on a commercial scale and to be widely used in wartime medical practice (Fleming, 1946).

In *Penicillium* the mycelium consists of freely-branching, septate hyphae with thin walls. The cells usually contain more than one nucleus. There is very profuse production of asexual, air-borne spores. Conidiophores grow vertically from the ordinary mycelium. They may be unbranched or branched. Each branch terminates in a brush-like (penicillate) tuft (Fig. 79). Each cell of the tuft is a sterigma. The sterigmata are uninucleate. In spore formation this

Ascomycetae—Plectomycetes

nucleus divides and one of the daughter nuclei thus formed moves into the narrower apex of the sterigma. This end portion is next cut off as a short, cylindrical cell. The protoplast contained in this cell secretes a wall surrounding the nucleus. As a result the spore formed lies inside either freely or with its wall fused to the containing wall of the terminal cell. Such spores are usually referred to as conidia, but they are really aplanospores. This process is repeated indefinitely, the additional cells being cut off in acropetalous succession. If the spore wall is free from the original wall

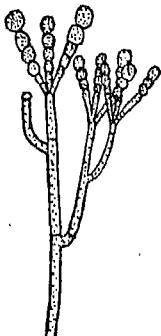


Fig. 79. *Penicillium*.
Part of brush-like
tuft formed by
branching conidio-
phore

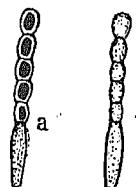


Fig. 80. *Penicillium* spp.
Two types of conidial
chain, showing a the
spore walls separated from the
original walls, b the spores
forming a continuous
row

then the spores in the chain appear slightly separated from each other, if not then they form a continuous row (Fig. 80a, b).

Sclerotia are sometimes formed. They resemble ascocarps; but have a very thick wall and contain no asci. It is reasonable to regard them as immature fructifications which have gone into the resting state. This switch over from one stage to another, contrary to the normal sequence of stages, is not uncommon among the fungi. It emphasizes that slight changes of environment may determine which phase of development the fungus will follow and that the demarcation line between the different stages is not clearly defined.

There is a tendency towards the formation of erect aggregations of conidiophores or coremia (Fig. 81).

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The conidial stages referred to *Aspergillus* are readily distinguished from those of *Penicillium* species by the swollen, often globose head of the conidiophore. The conidiophores arise from a definite foot cell. The greater part of the head of the conidiophore is fertile in *A. niger* van Tieghem. It

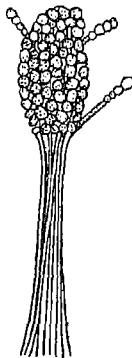


Fig. 81. *Penicillium*, Coremium formed from aggregated conidiophores

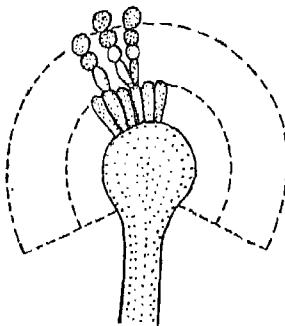


Fig. 82. *Eurotium*. Swollen conidiophore head of this type

bears a layer of cells all roughly perpendicular to the surface of the head. These are the primary sterigmata. Each bears one or more secondary sterigmata which, in their turn, produce the unbranched chains of conidia (Fig. 82). Some *Aspergilli* are also sources of antibiotics.

Strains of *A. fumigatus* Fresenius may be associated with tuberculosis in the human ear and with respiratory complaints.

ERYSIPHALES

The fungi contained in the family Erysiphaceae belonging to this order are obligate parasites growing on a wide range of flowering plants. The mycelium is formed largely on the surface of the epidermis of leaves, young shoots, flowers and fruits. Typically, it is almost entirely superficial and bears specialized branches or haustoria which penetrate the epidermal cells (Fig. 83). The mycelium is septate and the cells are uninucleate. Asexual reproduction is by

Ascomycetae—Plectomycetes

conidia which are formed in unbranched chains on unbranched conidiophores. The conidia are more or less oval or egg-shaped (Fig. 84). They germinate readily by one

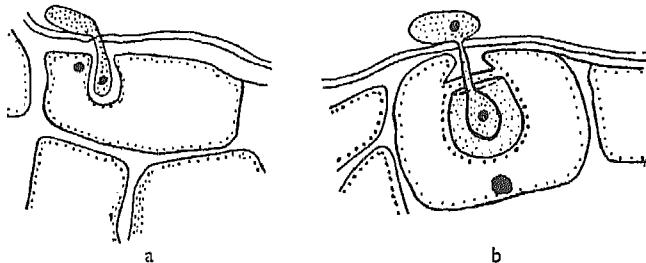


Fig. 83. *Erysiphe polygoni*. a Penetration of epidermal cell by haustorium which is surrounded by host cell wall; b later stage of penetration of epidermal cell by haustorium (after Smith, 1938)

or a number of germ tubes. The germ tube brings about reinfection. It produces a swollen portion at its tip. This becomes fixed to the cuticle by a sticky secretion and

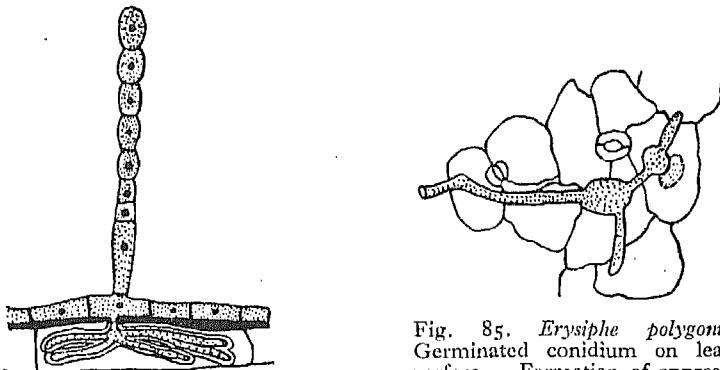


Fig. 84. *Erysiphe graminis*. Unbranched conidial chain. Branched haustorium in epidermal cell

Fig. 85. *Erysiphe polygoni*. Germinated conidium on leaf surface. Formation of appressorium and penetration of the leaf surface by hypha to the right (after Smith, 1938)

forms the appressorium, from which the haustorium develops (Fig. 85). The epidermal wall swells at the point of contact and the haustorium grows out as a branch, pushing the

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thickened epidermal wall in front of it so that a bulge is formed inside the epidermal cell. This bulge is usually pear-shaped. The nucleus from the normal part of the fungus cell passes into this haustorial swelling. Sometimes more than one haustorium is formed inside a single epidermal cell. These attacked cells are not killed for some time and a balance appears to be maintained between host and parasite.

Smith and Blair (1950) have found fully developed conidiophores of *Erysiphe graminis* f. *tritici* formed on wheat

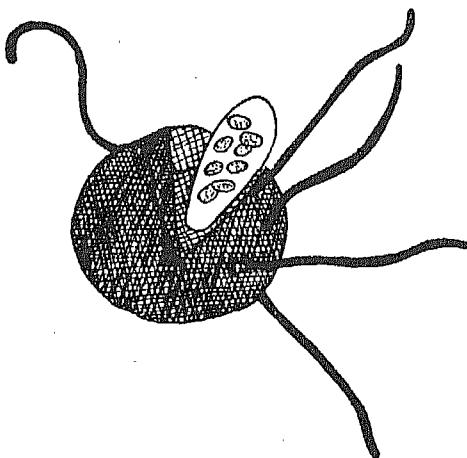


Fig. 86. *Sphaerotheca pannosa*. Cleistothecium with wall ruptured exposing the single ascus

leaves 6 days after the germination of the conidium which brought about infection.

The chains of conidia give a white, powdery appearance to the mycelium and are responsible for the general name Powdery Mildew which is commonly applied to the group. The term oidia is often used to describe conidia of this kind. Where the perfect (ascus) stage of the fungus is absent the generic name *Oidium* may be used to describe the conidial form, as in *Oidium chrysanthemi* Rabenh., the Powdery Mildew of cultivated chrysanthemums. It is normal to distinguish such species entirely on a host basis, as oidia on different hosts may be morphologically very similar.

In the majority of species, as the growing season of the host plant comes to an end, reproduction takes place by

Ascomyceae—Plectomycetes

means of ascii contained in closed fructifications or cleistothecia. In this case the cleistothecia have very definite walls. There is still no pore opening to the outside. Hyphae grow out from the walls to form appendages which are often characteristic in shape for a particular genus. The wall ruptures at maturity to expose the ascii, which open to release the ascospores. The latter germinate by germ tubes with appressoria and cause new infections. In *Sphaerotheca humuli* (DC.) Burr. the cleistothecium is reddish-brown in colour and spherical. It measures 58–120 μ in diameter. There is a single ascus within, which is broadly elliptical in shape, measures 45–90 \times 57–72 μ , and contains eight ascospores averaging 22 \times 15 μ (Fig. 86).

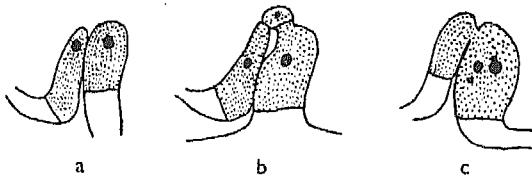


Fig. 87. *Sphaerotheca humuli*. a Uninucleate antheridium and ascogonium; b fusion of antheridium and ascogonium (adapted from Harper, 1895); c antheridium and ascogonium, showing both nuclei in the ascogonium (adapted from Harper, 1895)

The processes leading to the formation of the ascus were first described by de Bary for *Sph. humuli* (DC.) Burr. They have been redescribed and variously interpreted several times since. The antheridium and ascogonium arise near together from terminal cells of ordinary hyphae. The antheridium is small and is separated from its thin stalk by a cross wall. The ascogonium is larger and oval in shape. Both organs are uninucleate (Fig. 87a). They come in contact with each other and the wall between breaks down. The antheridial nucleus passes into the ascogonium (Figs. 87b, c). Varying accounts of subsequent events have been given. Some workers have maintained that the two nuclei fuse at once with subsequent division of the fusion nucleus so formed and others that they merely associate

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very closely. Nuclei are very small and detail is extremely difficult to interpret. Next, a short filament of three or four cells is produced from the ascogonium. This is called the ascogenous hypha. Its subterminal cell is binucleate and becomes the ascus (Fig. 88a). The two nuclei in the ascus fuse (Fig. 88b). The fusion nucleus divides three times to give the eight ascospore nuclei, round which the spores are formed in the usual manner. All workers agree that the first two divisions of the ascus nucleus constitute an ordinary meiosis. If a fusion has occurred in the ascogonium, however, there must be not only this normal meiosis but also a second

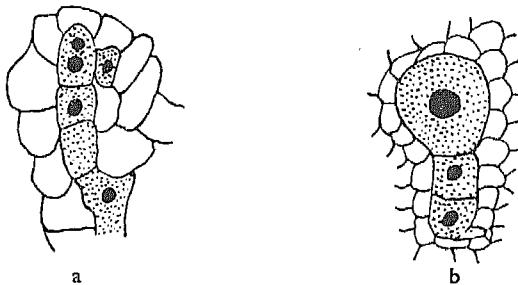


Fig. 88. *Sphaerotheca humuli*. a Ascogenous hypha with binucleate subterminal cell which will develop into the ascus; b fusion nucleus in young ascus (adapted from Harper, 1895)

reduction division at the third division of the nuclei to form the eight spore nuclei. Such a double reduction consequent upon the double fusion has been described in *Sph. humuli* (DC.) Burr. and in other Ascomycetace and named brachymeiosis. The reports of the discovery of this unique phenomenon stimulated cytological research among the Ascomycetace to a remarkable degree and it has been shown that brachymeiosis does not occur in many species investigated. It seems probable that the so-called fusion in the ascogonium is only a very close association of the two nuclei, followed by a slight withdrawal. If this is the correct interpretation, then the life history of this fungus contains a short phase, beginning with the fertilized ascogonium, including the ascogenous hypha and ending with the young

Ascomycetace—Plectomycetes

ascus, in which nuclei are associated in pairs forming what is called a heterokaryon or dikaryon. Cells of this type containing associated pairs of haploid nuclei of different origin are sometimes said to be diploid, but the use of this term is misleading. The only diploid cell in *Sph. humuli* (DC.) Burr. would appear to be the ascus, during the time it contains the fusion nucleus. The heterokaryotic mycelium is of much longer duration and greater importance in the majority of the Basidiomycetae.

While the development of the ascus is going on, a peridium has grown up round about it. This is a sheath of gametophytic hyphae arising mainly from the cell subtending the ascogonium. The outer hyphae are thickened and flattened to form the wall of the cleistothecium.

Six genera are usually distinguished within the family on the basis of the number of asci contained in the cleistothecium and the type of its appendages.

In *Sphaerotheca* there is a single ascus and the cleistothecium bears unbranched, curled appendages (Fig. 86). *Sph. humuli* (DC.) Burr. causes a serious disease of cultivated hops. It also attacks members of the Rosaceae. *Sph. pannosa* (Wallr.) Lév. is the common rose mildew and *Sph. mors-uvae* (Schw.) Berk. the American gooseberry mildew. This last is an example of a species in which the cells of the vegetative mycelium develop a dark colour and thick walls to form a resting mycelium which enables the fungus to survive the winter.

Erysiphe differs from the preceding genus only in the formation of several asci within each cleistothecium. They are produced by branching of the ascogenous hypha. *E. polygoni* DC. is common on many members of the Leguminosae and Cruciferae. *E. graminis* DC. is the mildew of wild and cultivated members of the Gramineae. It forms branched haustoria (Fig. 84).

Uncinula has stiff, thick-walled appendages with curled ends. They are formed on definite zones of the cleistothecium (Fig. 89). *U. necator* (Schw.) Burr. is the serious vine mildew. It first appeared in Britain in 1845 and was

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recorded in various European countries soon afterwards. Periodically it causes heavy damage. No cleistothecia were found for over 70 years. Their appearance is still sporadic and they have not been found in Britain. Before they were found, the imperfect (conidial) stage of the fungus was named *Oidium tuckeri*.

In *Phyllactinia* the appendages are equatorial, pointed and stiff, with a bulbous base (Fig. 90). They exhibit hygroscopic movements which cause the cleistothecia to fall off the host plant. There are also apical, short, much-branched outgrowths which become mucilaginous and cause the

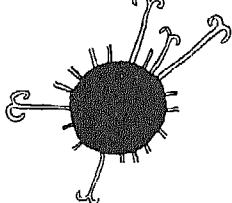


Fig. 89. *Uncinula*.
Cleistothecium with
stiff, dichotomously
branched append-
ages

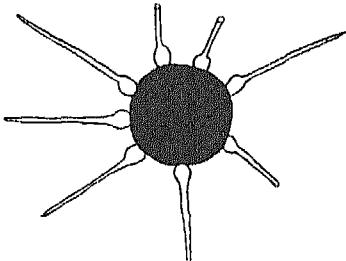


Fig. 90. *Phyllactinia*.
Cleistothecium with stiff,
equatorially-placed append-
ages each of which has a
bulbous base

cleistothecia to adhere to anything with which they come in contact.

Phyllactinia corylea (Pers.) Karst. does not have the typical epidermal haustoria. Branches of the mycelium enter the stomata and pass to the inter-cellular spaces where haustoria are formed in the mesophyll cells. This tendency is carried further in *Oidiopsis taurica* Lév. where the whole of the mycelium in the conidial stage is located inside the host tissues. In both these types appressoria still develop. They are regarded as examples of a limited tendency in the Erysiphales to pass from ectoparasitism to endoparasitism.

The Erysiphaceae show examples of specialization of physiologically distinct races within morphologically uniform species. Thus in *Erysiphe polygoni* DC. the mildew occurring

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on leguminous hosts will not infect members of the Cruciferae and *vice versa*. In *E. graminis* DC. the form on wheat will not infect barley or oats and so on. *Sphaerotheca humuli* (DC.) Burr. shows specialized forms on the different species and even microspecies within the genus *Alchemilla*. There is some evidence here that the fungi are evolving new forms to keep pace with the evolution of new microspecies in the higher plant hosts. Other species, too, furnish examples of the ability of these fungi to evolve forms suitable to attack previously immune hosts. *Sph. mors-uvae* (Schw.) Berk. at one time was unknown on black and red currants. Now both hosts may be attacked.

All powdery mildews may be controlled by applications of sulphur either as dust or in one or other of its liquid spray forms. It has to be borne in mind that some of the host plants are liable to suffer sulphur injury. Many gooseberry varieties for example are sulphur sensitive. An interesting new line of control for plant diseases in general is indicated by Felber and Hammer (1948) who inhibited the growth of *Erysiphe polygoni* DC. on bean plants by the use of an antibiotic substance, adidione, at a strength of 1–5 p.p.m. The antibiotic was isolated from beers in which streptomycin-producing strains of *Streptomyces griseus* were cultivated. Naturally-occurring antibiotic substances have recently been isolated from cereal straw by Grossbard (1948) and from the trunks of coniferous and deciduous trees by Erdtman and Gripenberg (1948) and Grosjean (1950) respectively. Any method which could stimulate the production of these substances by the higher plant would obviously increase its resistance to attack by fungi and other organisms. Crowdy and Wain (1950) have obtained promising results in the control of *Botrytis cinerea* Pers. (see p. 97) on broad beans by growing the plants in a solution of 10 p.p.m. of an aryloxyaliphatic acid. They regard the acid as a systematic fungicide, i.e. one which is translocated within the plant thereby conferring resistance to all parts liable to attack. Crowdy (1948) has similarly treated apple canker, and Zentmyer, Horsfall and Wallace (1946) report

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successful treatment of Dutch Elm Disease (*see* p. 87) by translocated compounds. Whether the chemicals supplied to the roots and translocated within the plant are always antibiotic or merely stimulate the production of antibiotic substances is not yet clear.

Yarwood and Jacobson (1950) have reported selective absorption of sulphur by the infected portions of leaves attacked by various fungi. When bean plants attacked by *Erysiphe polygoni* were exposed to vapours of sodium sulphide the treatment was lethal to the fungus and caused no injury to the host. The fact that selective absorption of the fungicide had taken place in the diseased areas was proved by the use of sodium sulphide containing radioactive sulphur (S^{35}). "Radioautographs" taken after treatment showed the S^{35} concentrated in the areas of the leaf occupied by the fungus pustules. That the S^{35} acts only as a tracer was proved by treating leaves with sodium sulphide vapour without S^{35} . The fungicide was just as effective in this case.

EXOASCALES

The fungi in this order still have no definite fructification. The asci are borne freely on the surface of the hosts which the different forms parasitize. There are obligate parasites on plant leaves, stems, flowers and fruits.

Taphrina deformans (Berk.) Tul. belonging to the Exoascaceae, occurs on peach, almond and nectarine leaves causing Leaf Curl (Fig. 91a). Spores seem to be present on the outside of the bud scales during winter and to bring about infection of the young leaves through the cuticle or the stomata when the buds open in spring. The septate mycelium produced inside the leaf is mainly concentrated between the epidermal and palisade layers. Its cells are binucleate. Attacked leaves become swollen and brittle and ultimately develop a red colour. Asci are formed above the epidermis, below the cuticle. They are cylindrical, measuring $25-40 \times 8-11 \mu$, and resembling the ends of ordinary hyphae. When mature, they push out forming a continuous row on the infected portion of the leaf (Fig. 91b).

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At this stage the ascus-bearing region appears to be covered with a grey bloom, like that seen on ripe fruit. Each ascus at first contains a single fusion nucleus, which later divides three times to give the eight ascospore nuclei. The ascospores are $3\text{--}4 \mu$ in diameter. They may germinate either within the ascus or after discharge from it, giving rise to numerous, minute conidia. The latter may continue the process further by producing numerous yeast-like cells. Some of the conidia are thick-walled, resistant and are capable of surviving on the host surface during winter. They bring about reinfection of the buds in spring.

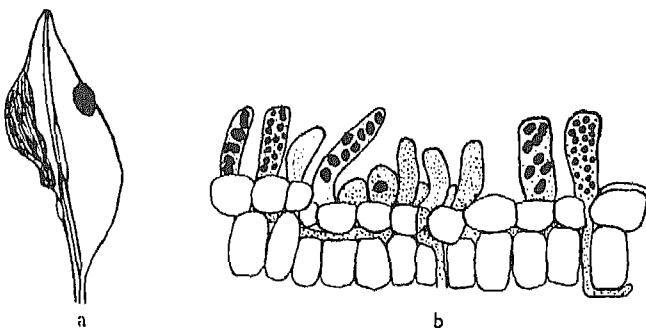


Fig. 91. *Taphrina deformans*, a Almond leaf deformed by the parasite; b row of exposed asci on almond leaf surface. The asci contain either 8 ascospores or numerous conidia produced from them by repeated division of the ascospore nuclei

It has been shown that single spores of this species are capable of bringing about reinfection and continuing the life cycle. Presumably, then, it is homothallic. Other species of *Taphrina* have been reported as heterothallic.

Leaf Curl may be controlled by the winter application of lime sulphur sprays which kill the resting spores on the outside of the dormant buds.

The family Protomycetaceae contains *Protomyces macrosporus* Unger, a parasite on *Aegopodium podagraria*. Conspicuous, pale swellings are produced on the leaf petioles, during summer. The swellings contain resting sporangia, $50\text{--}60 \mu$ in diameter with a thick, three-layered wall

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(Fig. 92a). The petioles decay over the winter and in spring the outer wall layer of the sporangium splits and the innermost is forced out as a sac (Fig. 92b). The multi-nucleate contents pass into the sac. A central vacuole develops, pushing the cytoplasm into a peripheral position (Fig. 93a). It is next cut up into uninucleate portions each

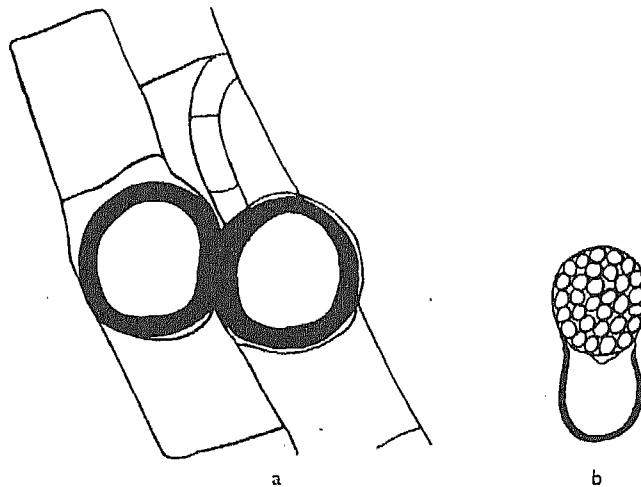


Fig. 92. a *Protomyces macrosporus*. Resting sporangia formed on a septate mycelium in the petiole tissues of *Aegopodium podagraria*; b *P. pachydernus* multinucleate contents of resting sporangium which have passed into emergent sac (b adapted from von Büren, 1915)

of which undergoes two divisions to form four spores. These are elongated and ellipsoid structures (Fig. 93b). They are discharged fairly violently from the sac by splitting of the wall (Fig. 93c). They put out short processes and fuse in pairs. The nuclei enter the bridge (Fig. 93d). It is not certain whether they fuse. The fused spores then germinate as a single structure which reinfects the host by pushing between the epidermal cells of the petiole. A septate, inter-cellular mycelium is produced, the cells of which are multi-nucleate. The resting sporangia are usually intercalary in position. They are formed by one segment of the hypha

Ascomycetae—Plectomycetes

receiving the contents of its neighbour. They are always multinucleate and the nuclei are often paired.

Nuclear details are obscure, the position of meiosis being uncertain. There is a difference of opinion as to whether epiplasm is left over in the formation of the spores in the sac and whether the nuclei fuse in the bridge formed when spores from the sac join. As a result of these obscurities the systematic position of the Protomycetaceae is uncertain.

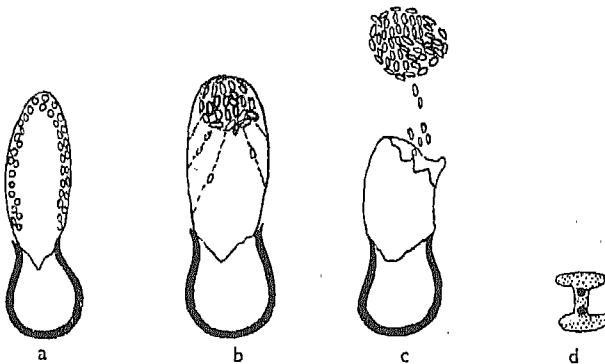


Fig. 93. *Protomyces pachydermus*. a Sac contents differentiated into peripheral cytoplasm and central vacuole; b differentiation of spores. *P. macrosporus* c violent discharge of spores by rupture of the sac wall; d fusion of spores and association of their nuclei in bridge which joins them
(adapted from von Büren, (a-c) 1915, (d) 1922)

The family is either regarded as belonging to the Phycoscytaceae, possibly standing near the Chytridiales or, if the resting sporangia are taken to be homologous with the fertile cells of the ascogenous layer in Exoascaceae, it is included in the Exoasccales. This is the position assigned to it above (Fitzpatrick, 1930). De Bary saw in this family a link between the Chytridiales and the Ustilaginales in the Basidiomycetaceae (see p. 137).

ASCOMYCETAE—PYRENOMYCETES

HYPocreales

HYPocreaceae: *Claviceps purpurea* (Fr.) Tul., the Ergot Fungus is an obligate parasite on members of the Gramineae. It attacks only the gynoecium where it forms resting sclerotia or ergots which replace some of the grains in an inflorescence.

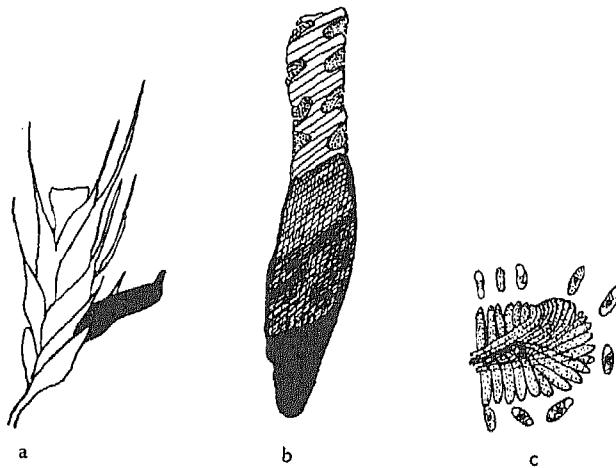


Fig. 94. *Claviceps purpurea*. a Ergot on part of ear of rye; b infected rye ovary in *Sphacelia* stage; c upper portion of ovary shown in b, palisade-like conidiophores with conidia

These ergots are larger in size than the grains which they replace but correspond roughly to them in shape. In rye they may be up to 3 cm. in length (Fig. 94a). Infection of the grass flowers takes place at the time of pollination by means of thread-like ascospores which are often carried by air currents. The length of time which its flowers remain open affects the susceptibility of a grass species to attack. Thus, rye flowers remain open for a longer time than those of

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wheat and the former plant is more often attacked than the latter. The ascospores germinate on the stigma and produce hyphae which pass down the style to the developing ovary. On the upper part of that organ masses of conidiophores are developed forming a palisade-like layer. Numerous small conidia are cut off. They measure a few microns in diameter (Figs. 94b, c). They are mixed with a sweet liquid. This conidial stage was called *Sphacelia segetum* Lév. before its

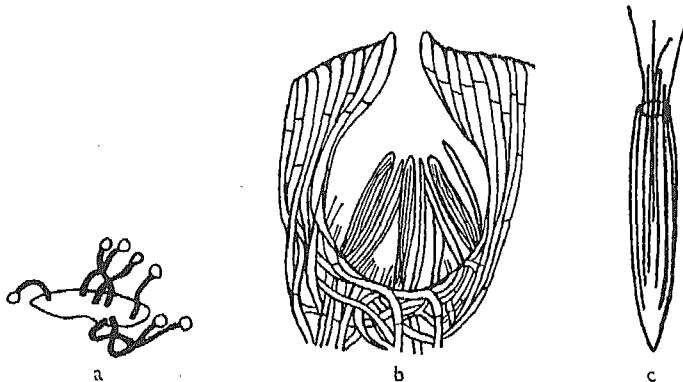


Fig. 95. *Claviceps purpurea*. a Mature ergot which has produced 7 stromata; b part of stroma head with ostiolate peritheciun containing asci and paraphyses; c ascus discharging thread-like ascospores

connexion with the perfect, ascus stage was realized. It is still called the *Sphacelia* or Honeydew stage. The sticky liquid is attractive to insects which visit infected flowers and mechanically spread the conidia to uninfected ones. Later the production of conidia in this upper region dies down and the ovarian tissue is replaced from below upwards by an interwoven mass of hyphae. The structure becomes hard with a dark, thick wall and forms the sclerotium or ergot, which projects conspicuously from the glumes. It is shaken from the grass inflorescence with the normal, ripe grains in autumn and falls to the ground. In late spring the ergot germinates. Its germination is helped by previous freezing. A number (frequently about six) of pale drums tick-like stromata is produced (Fig. 95a). Each is up to 25 mm.

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long and has a cylindrical dark purple stalk and a rounded pinkish head in which are embedded numerous perithecia (Fig. 72). The position of each perithecium is marked by a papilla which surrounds the ostiole. Each contains numerous club-shaped ascii, arising towards its base, interspersed with slender paraphyses (Fig. 95b). Thread-like ascospores, measuring $60-70 \times 2 \mu$, are released from the ascus and thence by the ostiole to the surface of the stromatic head (Fig. 95c). They may be distributed either by splashing rain drops or, under dry conditions, by wind, to open grass flowers of the same species as that on which they are produced.

There are a number of specialized races within the species *Cl. purpurea*; but the specialization is not very extreme for the same race attacks rye, wheat, barley and a number of pasture grasses.

Ergot grains contain poisonous alkaloids which affect muscle action and produce other disease symptoms in humans and animals, notably gangrenous conditions of the extremities. Where bread made from infected rye is the staple diet or where farm stock have access to infected grasses, outbreaks of ergotism occur. The symptoms produced in humans are described by Barger (1931). Ergot is employed in medical practice and fields of infected rye are grown in Spain and other parts of Europe to provide a source of the drug.

Nectriaceae: *Nectria cinnabarina* (Tode) Fr., the Coral Spot Fungus, grows and produces fructifications on tree branches, usually after their death. But it may act as a facultative parasite entering healthy tissue from dead snags and killing back the branches usually from near the apex. It is common on sycamore, lime, horse chestnut, apple, gooseberry and currant. Sometimes it causes a serious disease of red currants. It cannot attack healthy tissues except by growing from dead areas. The septate mycelium is found in all tissues and is frequent in the vessels. It consists of fine, colourless hyphae which mass at intervals in the cortex to form a pseudo-parenchyma. This mass ruptures

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the bark, emerging as a fairly-conspicuous, pinkish stroma, 1–2 mm. across, surrounded by the reflexed bark (Fig. 96a). This type of structure is called a sporodochium and consists of a mass of hyphae, raised above the level of the mycelium, the individual hyphae standing close together without being laterally united. Branched conidiophores are produced all over its surface. The conidia are hyaline, one-celled, measuring $4-6 \times 2 \mu$ (Fig. 96b). They are wind

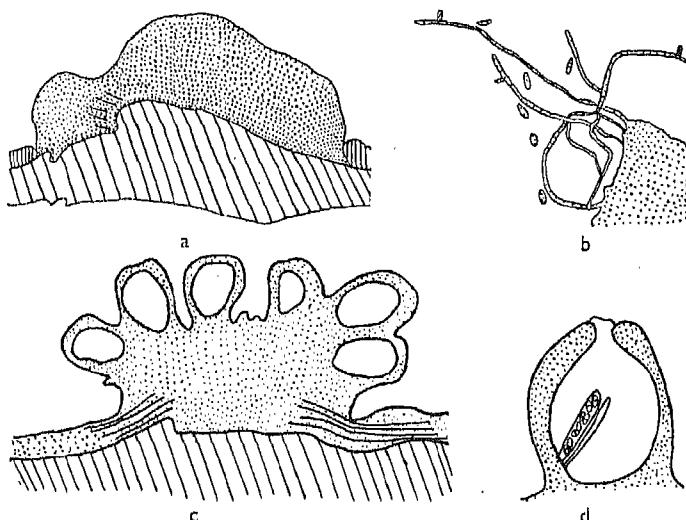


Fig. 96. *Nectria cinnabarina*. a Conidial stroma (sporodochium) emerging from bark of a dead sycamore branch; b surface region of conidial stroma showing hyphae and unicellular spores; c perithecial stroma; d diagrammatic drawing of a single perithecium and one of the contained asci

distributed. Subsequently, red perithecia are produced on the same stroma. The upper part only of each perithecium projects from the stroma (Fig. 96c). Each is about 0.5 mm. in diameter and contains numerous asci which measure $50-90 \times 7-12 \mu$. The asci contain eight, two-celled, colourless ascospores, $12-20 \times 4-6 \mu$ in size. The spores are obliquely arranged in the ascus (Fig. 96d). They are discharged as in *Claviceps*.

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Nectria galligena Bres. has a similar life history. It causes apple and pear canker. This is a serious disease, as the cankers, if unchecked, will ultimately girdle the stems and bring about the death of the trees (Fig. 97). If plants are

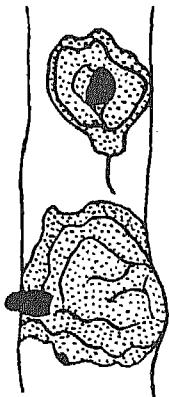


Fig. 97. *Nectria galligena*. Cankers centred round dead branch bases on apple stem

badly infected they should be removed and all cankered parts burned. Less extensive cankers may be cut out in winter. These and other pruning wounds should be painted over to prevent infection by spores. Spraying with Bordeaux Mixture, to which a good adhesive and wetting agent has been added, prevents infection through small openings, particularly leaf scars.

SPHAERIALES

The fungi in this group are distinguished from those in the previous order by possessing dark coloured, brittle fructifications. The distinction between the two is not absolute. Thus *Neurospora* which has light brown perithecia is usually placed here in Sordariaceae but sometimes included under Hypocreales in Nectriaceae.

In Ceratostomataceae the genus *Ophiostoma* contains some species in which the conidial stage consists of hyphae united closely into solid columns known as coremia. The one-celled conidia are budded off from the upper, head end. Such

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conidial stages were originally described as species of the imperfect genus *Graphium*. The conidial stage is still frequently referred to as the *Graphium* stage although its connexion with the perfect *Ophiostoma* stage may now have been established.

Ophiostoma ulmi (Buism.) Nanf. is the fungus responsible for a serious die-back of elms, usually referred to as Dutch Elm Disease. The coremia are about $1\frac{1}{2}$ millimetres high and the branched conidiophores produce, at the top, pear-shaped unicellular conidia, measuring $3 \times 2 \mu$.

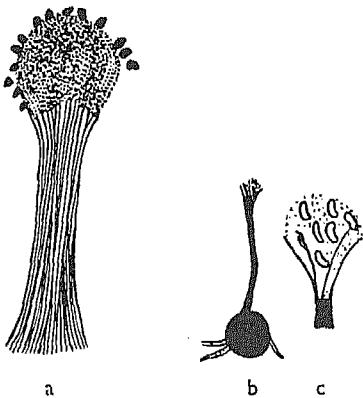


Fig. 98. *Ophiostoma ulmi*.
a Conidium-bearing hyphae united to form a coremium;
b perithecioid with long neck;
c tip of perithecioid neck showing discharge of ascospores in mucilage produced by disintegrating ascus walls (b and c after Clinton and McCormick, 1936)

and massed together into a glistening head (Fig. 98a). The perithecia are $105-135 \mu$ in diameter and each is surmounted by a long, tapering, hair-like neck measuring up to 350μ (Fig. 98b). The egg-shaped asci are embedded in mucilage. Their walls disintegrate (become fluid) early. They contain, normally, eight unicellular, hyaline spores measuring $4.5-6 \times 1.5 \mu$. The spores are squeezed out through the neck in a mucilaginous mass (Fig. 98c). The species is heterothallic. Mycelia are of two complementary types. Certain mycelia produce sclerotium-like bodies. These have been interpreted as being perithcia whose development has been checked by the absence of a complementary mycelium necessary to bring about the nuclear associations and fusions leading to the maturation of asci.

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Dutch Elm Disease is a vascular disease. The wood of the current year particularly is attacked. Water transport is interfered with and parts of the crown of the tree die back. The spores are spread by small bark beetles. In Britain the disease is almost confined to England and its range corresponds generally with that of the vector beetles (*Scolytus spp.*) in this country. Coremia and perithecia both occur in cracks in the bark and in the galleries bored by the beetles.

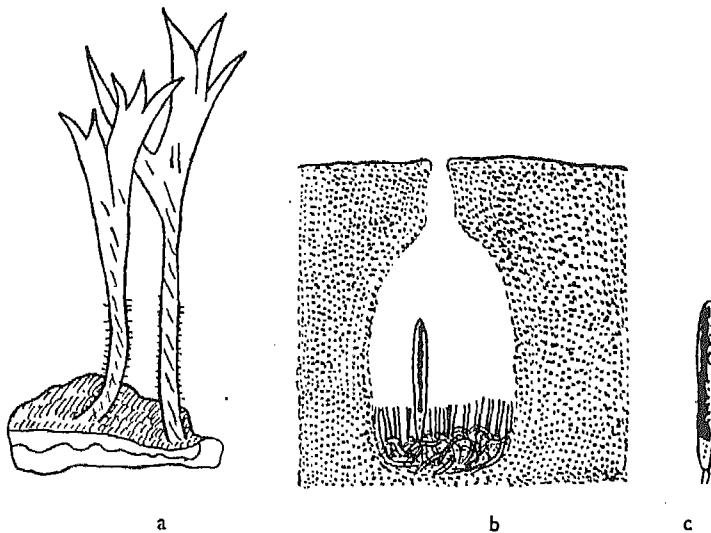


Fig. 99. *Xylaria hypoxylon*. a Dichotomously-branched stromata; b perithecium; c single ascus with 8 dark, one-celled spores

Attempts at control of the disease have usually been based on control of the beetles. Stringent measures have met with considerable success in the United States, where, in Philadelphia, as long ago as the early 1930s, spraying was carried out from aeroplanes in large scale attempts to control the disease by killing the insect vectors. A considerable amount of work has been carried out both in America and in Europe on the selection and breeding of resistant forms of elm.

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In the Xylariaceae the stroma is well-developed. It is stem-like in many species. The fungi are saprophytes on decaying branches or tree trunks or sometimes on the ground. When the mycelium is growing in wood the occupied regions are often clearly delimited from the uninfected parts by dark lines. Microscopical examination shows that the dark portions of the tissues are filled with dark, thick-walled hyphae forming a layer comparable with the wall of a sclerotium. The name pseudo-sclerotium is applied to the area bounded by the black line.

Xylaria hypoxylon (L.) Grev., one of the Candle Snuff fungi, is regarded as a highly evolved form. It has a fairly thin, more or less dichotomously branched stroma, 3-4 cm. tall (Fig. 99a). Minute, oval conidia are produced first on the upper part. They turn the surface whitish grey. The lower part of the stroma is dark and hairy. Later it contains the perithecia (Fig. 99b). These form a distinct layer entirely embedded below the surface. In each perithecium the asci develop in a cavity in the stromatic tissue. Each ascus contains eight dark, one-celled spores (Fig. 99c).

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IN THIS last division of the Ascomycetae the asci are formed in a hymenium exposed at maturity on the surface of an apothecium. The hymenium consists of a layer of cylindrical asci interspersed with sterile hyphae known as paraphyses. Some species reproduce also by conidia. The apothecia are frequently cup-shaped. In early classifications all fungi with cup-like fructifications were placed in the genus *Peziza*. The species referred to here are now usually divided into four orders and a number of families.

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Much of the detailed work on the reproductive processes of the Ascomycetaceae has been carried out on discomycetous fungi and, as a matter of convenience, the main trends will be illustrated by examples within this subclass. The exact systematic position ascribed to these fungi is not of great importance in this connexion and the question of reproduction may well be dealt with before that of classification.

Pyronema confluens Tul. may be taken as an example of those forms in which both antheridia and ascogonia are

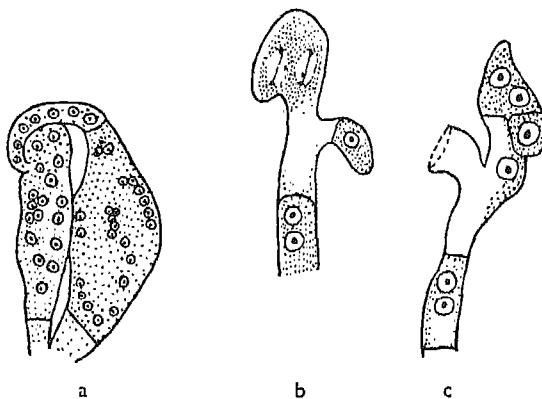


Fig. 100. *Pyronema confluens*. a Multinucleate antheridium and ascogonium, the latter is surmounted by a trichogyne; b binucleate, crosier-shaped portion of ascogenous hypha; c ascogenous hypha with binucleate subterminal and uninucleate terminal and supporting cells, produced by the completion of the nuclear divisions shown in b (after Gwynne Vaughan and Barnes, 1937)

produced and function normally. In the mass of hyphae coming together to form the fructification it is possible to make out a number of female branches or archicarps each consisting of a stalk of several cells with a terminal ascogonium (Fig. 100a). For each ascogonium there is also present an antheridial hypha with a terminal antheridium (Fig. 100a). Ascogonium and antheridium come to lie side by side. The ascogonium is surmounted by a trichogyne

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which curls over the antheridium. Both organs are multi-nucleate. Fusion takes place. The majority of the antheridial nuclei pass through the trichogyne to the ascogonium where they pair closely with the ascogonial nuclei. From the ascogonium now arise a number of branches termed ascogenous hyphae. In each of these the terminal portion ultimately becomes binucleate and crosier-shaped (Fig. 100b).

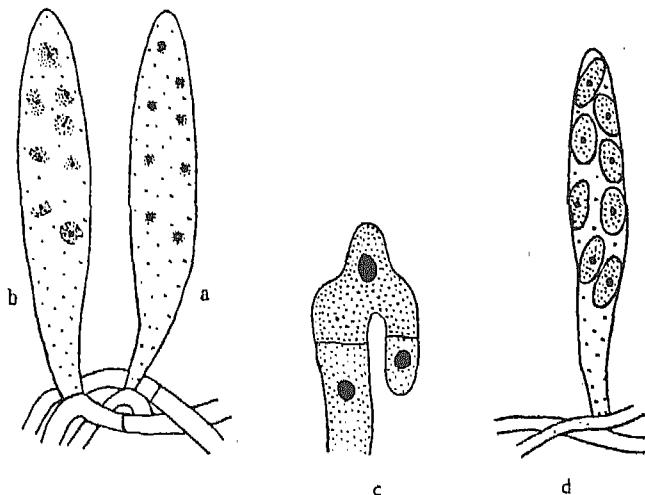


Fig. 101. *Pseudopeziza medicaginis*. Diagrammatic drawing of a ascus containing 8 nuclei formed from the division of the fusion nucleus; b ascus showing spore formation round the 8 nuclei; c fusion nucleus in subterminal cell of ascogenous hypha; and d mature ascus

The pair of nuclei, one from the antheridium, one from the ascogonium, divide. The division is accompanied by septum formation so that uninucleate apical and stalk cells are cut off from a binucleate cell lying between (Fig. 100c). The nuclei in the binucleate crook cell now fuse (Fig. 100c). The crook cell develops into the ascus, the fusion nucleus dividing three times to give the eight ascospore nuclei (Fig. 100a, b, d).

In *Pyronema domesticum* (Sow.) Sacc. both types of organ are present; but the ascogenous hyphae may begin to grow

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out before fusion of antheridium and ascogonium takes place. In *Lachnea stercorea* (Pers.) Gill. both are present also and fusion between them takes place; but no antheridial nuclei pass to the ascogonium. In *Lachnea cretea* (Cooke) Phil. and *Humaria granulata* Quél no antheridium is formed and, in the latter species, the ascogonium has no trichogyne. *Pseudopeziza trifolii* (Fr.) Fuckel shows only a non-functional ascogonial coil. In *Humaria rutilans* (Fr.) Sacc. and *Peziza vesiculosa* Bull. ex Fr. both antheridium and ascogonium are entirely suppressed. Prior to the formation of ascogenous hyphae and asci, pairing and fusion take place between cells indistinguishable from those of the ordinary vegetative hyphae. As well as the tendency to reduce the sexual organs which is illustrated by this series, the development of apogamy and still more of heterothallism should be noted. Thus *Humaria granulata*, which has no antheridia, is self-sterile. The ascogonia fail to develop in single spore culture. If a complementary mycelium is introduced, however, fusions occur. A sheath of hyphae then surrounds the ascogonium which buds out ascogenous hyphae and proceeds to ascus production.

PHACIDIALES

The apothecial fructifications in this order are at first enclosed in a well-developed stroma. The hymenial layer is exposed as it reaches maturity by splitting of the stromatic tissues in various ways. The shape of the fructifications varies in the different genera from elongated, opening by a narrow slit, to round with stellate opening. The species are parasites.

Rhytisma acerinum (Pers.) Fr., the Tar Spot fungus belongs to the family Phacidiaceae. It causes black blotches on leaves of sycamore and other species of *Acer* (Fig. 102a). The covering over the hymenium early consists of the host epidermis and some fungal tissue (Fig. 102b). Infections are limited in extent, never reaching more than $2\frac{1}{2}$ cm. in diameter. The same leaf, however, often bears a number of infections. Infection of the leaves takes place shortly after

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the buds open. It is caused by long, needle-shaped ascospores which are carried by wind currents. The spores become attached to the cuticle on the lower surface of the leaf by means of their sticky, gelatinous sheaths. A single germ tube per spore penetrates through a stoma. Once penetration is secured the germ tube branches and gives rise to a mycelium which is almost entirely intracellular. The chlorophyll is destroyed in the cells which are attacked. Ultimately the tarry spot develops due to the abundant

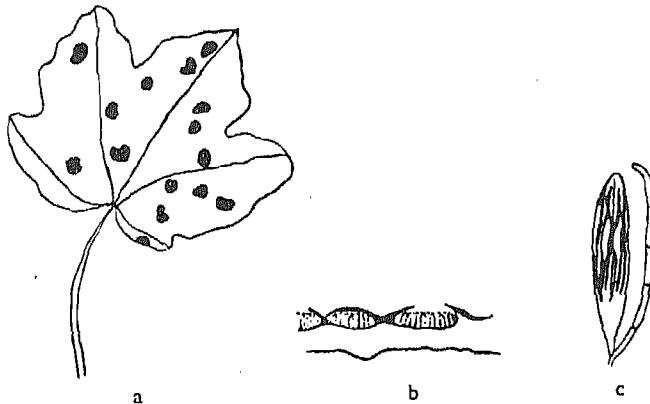


Fig. 102. *Rhytisma acerinum*. a Infected sycamore leaf; b T.S. sycamore leaf showing hymenia covered by host epidermis and fungus tissues; c single ascus with thread-like ascospores

hyphae, particularly in the palisade cells, developing black colour. In summer, from June to the end of August, round dots appear on the surface of the spot. These mark the position of ostioles by which minute conidia (spermatia) are exuded as thin milk. They are $6 \times 1 \mu$. They do not germinate. Infections do not seem to cause premature defoliation. Well-marked ridges develop in the tar spots on the fallen leaves in April to May. This time the surface splits to expose the hymenium of clavate asci, $120-130 \times 9-10 \mu$, and hyaline, filamentous paraphyses, which are curled at the ends (Fig. 102c). The eight ascospores are unicellular, uninucleate, filiform and hyaline. They

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measure 65–80 × 2–3 μ . Each has a gelatinous sheath. They resemble bundles of needles inside the ascii. The ascii rupture, discharging the spores violently. The latter reinfect the young leaves. These spores are readily borne upwards by air currents. They have been collected at heights up to 19,000 feet in viable condition.

There are specialized races within this species on the different species of *Acer*. It is quite a common thing to see *Acer pseudoplatanus*, the sycamore, heavily infected while *Acer platanoides*, the Norway maple, alongside is free from infection.

A lot could be done towards controlling this disease by removing all fallen, infected leaves. No doubt this would be done if the disease was of economic importance. Spraying with a copper-containing spray has been recommended.

PEZIZALES

In this order the apothecium is not enclosed during development. It takes the form of a cup. The species are saprophytes. Pezizaceae contains the name genus *Peziza*. Many of the cup fungi occur on decaying organic matter or on the soil surface. They vary in size up to 15 cm. in diameter. The hymenium is slightly covered when young though fully exposed at maturity. *Humaria granulata* forms bright red apothecia on dung. In the family Pyronemataceae the hymenium is exposed during development. *Pyronema confluens* grows on burned ground and *P. domesticum* on damp walls. Both produce pink apothecia a few millimetres in diameter.

HELOTIALES

In this order the apothecia are stalked. There is usually production of conidia as well as of ascospores.

Helotiaceae:—*Dasyphypha wilkommii* (Hart.) Rchm. is the Larch Canker fungus. It is a wound parasite causing a serious disease of larch (Fig. 103a). Its effects are worst on seedlings and young trees. Damage caused is slight if the trees are more than 40 years old when attacked.

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Stromata are produced growing through the bark round the cankered regions, as short-stalked structures 2–5 mm. across which are pale yellow in colour outside and orange-red inside (Fig. 103b). The ascii are club-shaped, 150–200 × 10–14 μ , and contain a single row of eight elliptical spores 20–23 × 9–10 μ (Fig. 103c). Smaller, paler fructifications are formed among the apothecia. These contain conidia (spermatia) which will not germinate. Here, as elsewhere, the suggestion has been made that they are homologous

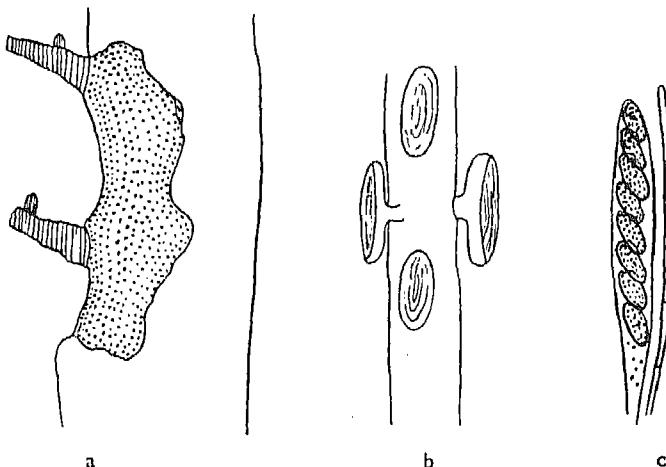


Fig. 103. *Dasyphypha wilkommii*. a Canker on larch stem centring round dead twig; b short-stalked apothecia on dead larch twig; c ascus with spores

with antheridia and that in the course of evolution they have lost their original function. No ascogonium is formed.

In assessing the importance of *Dasyphypha wilkommii* as a canker-producer it must be remembered that much canker damage to larch in this country is attributable to frost injury. The fungus may be present growing as a saprophyte on killed stems. The use of hardy varieties suitable for local conditions is a valuable control measure. Where the fungus is the primary cause of canker the most common means of attack is by ascospores which bring about infection of dead

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stumps of died-back branches of dormant buds. The mycelium spreads into healthy tissue, attacking it by enzymes. There is a big production by the wood cambium of "wound wood" parenchyma cells which may become lignified in an attempt to isolate the infected region. If the attempt is successful, normal xylem is again formed. The excluded infection dries up and finally drops off. If the attempt does not succeed a canker is formed; but the wood cambium makes a series of attempts during which successive layers of "wound wood" parenchyma are produced. Either the fungus is finally excluded or else the wood cambium is reached and growth is completely checked in the attacked part. In seedlings the tree is completely girdled and killed.

Sclerotinia contains species which form sclerotia from which stalked apothecia develop (Fig. 104a). Most species form asexual conidia and some also produce spermatia or microconidia which are functional and homologous with antheridia. The genus is of special interest in this connexion because three types of sexual behaviour have been distinguished among its species (Groves, 1951). In *Sc. sclerotiorum* (Lib.) de Bary a haploid thallus grown from a single ascospore bears both male and female organs and these are interfertile. This is the homothallic, self-fertile condition. In *Sc. gladioli* (Massey) Drayton both organs are again formed on the same monospore thallus but they are intersterile—the homothallic, self-sterile state. Compatibility is determined by a single pair of allelomorphs. In *Sc. narcissi* four of the eight haploid ascospores contained in any ascus give male thalli and four produce female thalli. Spermatia from a male thallus must be transferred to a female thallus before fertilization is effected. There is thus sexual dimorphism and this species is therefore truly heterothallic.

Sclerotinia fructigena Aderh. and Ruhl. causes Brown Rot and Spur Canker of apples, plums, etc., in Europe generally. In America and Australasia similar symptoms are produced by *Sc. fruticola* (Wint.) Rehm. In Britain only the imperfect, conidial stage of the fungus occurs; this is called *Monilia fructigena*. The conidia are rather barrel-shaped and formed

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in chains (Fig. 104b). They are freely produced on attacked fruits and twigs, forming brown pustules 3–5 mm. in diameter. Individual conidia average $22 \times 13 \mu$. The conidia are carried by air to uninfected parts of the host plant. The fungus spreads rapidly by this means. It is also spread by contact from infected fruit to others in the same group on the tree or in storage. Infected fruits tend to dry up and become mummified. They fall to the ground and provide the means by which the fungus can survive the winter. Fresh crops of conidia are formed in the spring and bring about new infections. Where apothecia occur, they

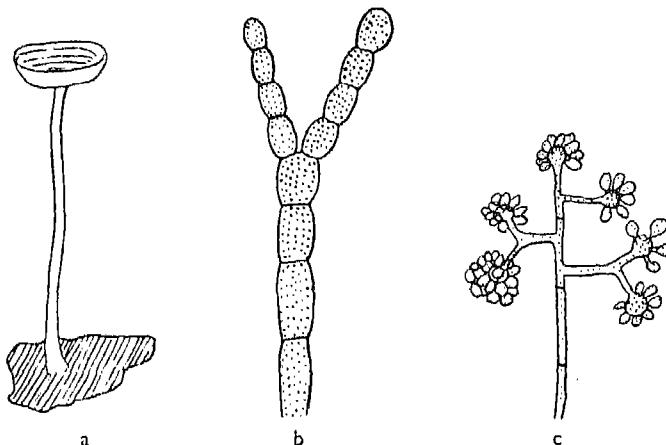


Fig. 104. *Sclerotinia*, a Stalked apothecium developing from portion of a sclerotium; b conidial chains of a *Monilia* stage; c conidiophore of a *Botrytis* stage

arise, also in spring, from the mummy fruit, half buried in the soil. They are stalked, brownish structures up to 7 mm. in diameter. Ascii average $156 \times 10 \mu$, with unicellular, ellipsoid ascospores measuring $12 \times 6 \mu$.

This and similar diseases may be controlled effectively by the removal of all infected material both growing on the tree and on windfalls during the winter.

Botrytis cinerea Fr. is the conidial stage of a sclerotoid *Sclerotinia* which causes a serious disease of grape vines. In

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the conidial stage it is referred to as Grey Mould. In this country Grey Mould occurs on a wide variety of woody and herbaceous plants. It causes a die-back of gooseberries and under humid conditions it causes moulding of tomatoes, lettuce, etc., under glass. Entry to living tissue is gained through dead snags and wounds. Living tissues are killed in advance by toxic secretions from the hyphae. Apparently, growth forced with nitrogenous fertilizers is particularly susceptible to attack. Conidia are borne on branched conidiophores and form dense tufts, suggesting bunches of

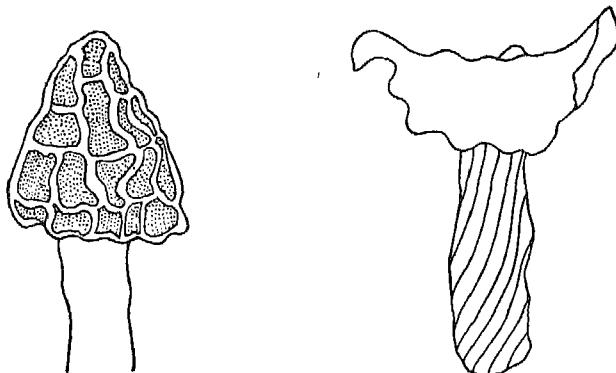


Fig. 105. *Morchella esculenta*. Stalked fruitbody with hymenium in the hollows of the cap

Fig. 106. *Helvella crispa*. Fruitbody with grooved stalk and hymenium on saddle-like head

grapes (Fig. 104c). Each conidium is produced on the end of a small sterigma. The mass is grey to brown in colour. Sclerotia are black in colour, rough in surface and irregular in shape, up to 6 mm. in length. They are formed in the decaying tissues. Two strains which differ markedly in their tendency to produce sclerotia and slightly in the dimensions of their spores have been isolated from lettuce. The "A" strain produces more sclerotia and fewer conidia averaging approximately $11 \times 7 \mu$. The "B" strain forms fewer sclerotia and more spores which average approximately $9.5 \times 8 \mu$.

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Pseudopeziza trifolii (Fr.) Fuckel, belonging to the Mollisiaceae, causes a leaf spot of cultivated clovers. It does not seem to produce pycnidia or conidia. The small apothecia break out through the leaf surface bearing a dense hymenium of ascospores and paraphyses. There are neither antheridia nor ascogonia formed, only a non-functional ascogonial coil.

HELVELLALES

Helvellaceae contains the much-prized edible morels. The fruitbody is stalked. The hymenium is folded in varying

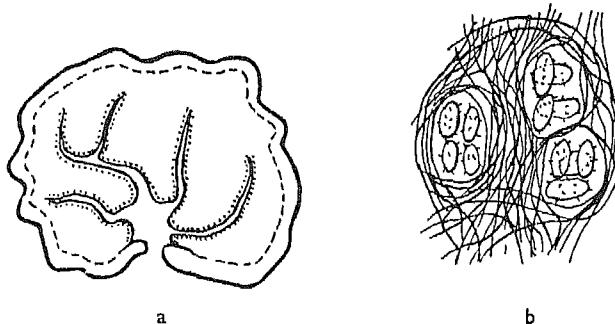


Fig. 107. *Tuber*. a Largely-closed fruitbody with hymenium lining internal cavities; b four-spored asci embedded in interwoven hyphae

degrees. In *Morchella esculenta* Pers. ex Fr. the hymenium is in the hollows of a cap (Fig. 105). The ridges of the cap and the stalk are sterile. In *Helvella crispa* Fr. the stalk is deeply grooved and the cap almost saddle-like with the hymenium on its upper surface (Fig. 106).

TUBERALES

In the family Tuberaceae there are underground forms, which often form mycorrhiza with trees. They have curious tuber-like fructifications up to 8 cm. in diameter. The hymenium is borne more or less inside the fruitbody. It is possible to trace within the order all stages of closing of the fructification from forms quite like those occurring in the

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Pezizales to *Tuber*, which shows well the degeneration of the group. Its asci are produced endogenously and do not form a single hymenial layer (Fig. 107a). The asci are rounded in shape and no longer distribute the spores, which may be reduced even to one per ascus (Fig. 107b). Distribution of spores is due to animals, especially to rodents which are able to smell out the fructifications. The fruitbodies are highly prized as food. They are known as truffles. In southern Europe those of *T. aestivum* Vitt. especially, are hunted with the help of dogs or pigs, as a commercial enterprise.

14

ASCOMYCETAE—RELATIONSHIPS

WHILE the possibility of a separate flagellate ancestry for the Ascomycetae cannot be excluded altogether, there are two other main views on their origin. The first was originally suggested by de Bary. It derives the Ascomycetae from the Phycomycetae and regards the simplest forms as most closely linked with the Zygomycetes. It will be dealt with in more detail later. The second view is that first mooted by Sachs. This lays stress on the similarity in form between antheridium and ascogonium with trichogyne in the Ascomycetae on one hand and the sexual organs in the Florideae on the other and between ascogenous hyphae and ascocarps in the former and sporogenous filaments and carpospore fructifications in the latter. It derives the more complex Ascomycetae from red algal ancestors and the simpler Ascomycetae from the complex by reduction. At first sight this is a most attractive theory but there is no evidence that many of the less complex Ascomycetac are reduced forms and the origin of the Basidiomycetae becomes very difficult to understand. De Bary's view offers no

Ascomycetae—Relationships

simple explanation either, and necessitates belief in the parallel development of similar structures in the Ascomycetaceae and Florideae. It does, however, make it possible to trace throughout the Ascomycetaceae a rise in complexity of the sexual apparatus followed by its suppression which is linked with an increase in efficiency of methods designed to protect and ensure the distribution of the ascospores. On this ground it seems the better view to accept.

In the description of the species of Ascomycetaceae in the preceding pages simple forms typified by *Eremascus fertilis* were dealt with first. In this fungus identical protuberances, formed by what appear to be two ordinary, uninucleate cells, fuse and the fusion cell, the zygote, gives rise to the ascus directly. This shows many similarities with forms such as *Endogone* among the Zygomycetes. The fundamental difference is in the method of spore formation. The main lines of development from *Eremascus* involve first the separation of the fusion of the gametangia from the fusion of their contained nuclei, secondly the development of hyphae forming tissues to protect the sex organs and the products of their fusion, and thirdly, the increase in complexity of the female branch, *i.e.* ascogonium and trichogyne. There is no increase of the antheridium to keep pace with this last. The male organ degenerates and disappears, though in some cases its function is taken over by the spermatium. This degeneration is followed by that of the ascogonium, till the production of morphologically distinct sexual organs of both types is suppressed.

Reverting to the first of the three lines of development, *Sphaerotheca humuli* illustrates this by its development of the short ascogonial filament between the fused sex organs and the production of the ascus. Other genera in the same family have branching of the ascogonial filament with production of several asci and point the way by which a peritheciun with a number of asci might have been evolved from a cleistothecial type. Although *Taphrina* is regarded by most authorities as a reduced, specialized type, its row of asci fully exposed at maturity does indicate

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a possible intermediate type in the evolution of the apothecium.

The perfect, complex sexual apparatus of *Pyronema confluens* and that of representative forms in the reduction series leading to the disappearance of these organs have been described on pp. 90-92. Mention of another phenomenon of great evolutionary significance should also be made. In *Pyronema confluens* and many other Ascomycetae the appearance of the subterminal binucleate cell which becomes the ascus, is associated with the formation of the hook or crosier. Two cross walls are laid down by which two uninucleate cells are formed—one the apical the other the stalk cell (Fig. 100c). These lie close together and in this species as elsewhere fusion between them may occur. In certain higher forms, e.g. *Helvella*, the fusion is the rule. The nucleus from the terminal cell passes into the stalk cell to pair with that already present. This phenomenon bears a very striking resemblance to the formation of clamp connexions in the Basidiomycetae referred to on pp. 9-10 and 106. It is strong evidence in support of the theory that those Ascomycetae which have lost their morphologically distinct sexual organs by reduction and have developed and retained the formation of the crosier in connexion with ascus formation, stand closest to and have led to the Basidiomycetae.

BASIDIOMYCETAE—GENERAL AND CLASSIFICATION

THROUGHOUT the group the mycelium is septate. In the typical members (Homobasidiomycetes) it usually bears clamp connexions (*see* pp. 9-10). These are regarded as homologous with the hooked, crosier hyphae whose appearance precedes ascus formation in the Ascomycetae. Hence

Basidiomycetae—General and Classification

those species which possess them are accepted as standing nearest of basidiomycete fungi to the Ascomycetae. The sporangium is the basidium which bears the typically four spores externally. A considerable development of pseudo-parenchyma in connexion with the growth of the reproductive stages is the rule. Hence many Basidiomycetae have large fructifications often of a very definite shape, as in the toadstools and in the bracket fungi. But, throughout, there is great diversity in the form of the fructification, ranging from the row of naked basidia in *Exobasidium* to the frequently fantastically shaped epigaeous and hypogaeous fruitbodies of the Gasteromycetales. The reduction of the sexual process is carried still further than in the Ascomycetae. Sexual organs are not recognizable in the Homobasidiomycetes and the sexual process is represented throughout this group only by the fusion of nuclei contained in hyphae similar in appearance to those of the ordinary vegetative mycelium.

The Basidiomycetae may be divided most conveniently into Homobasidiomycetes, including those fungi with an undivided basidium, and Heterobasidiomycetes, composed of the orders in which the basidium is divided by septa. Because the undivided basidium more closely resembles an ascus than does the septate one and because members of the Homobasidiomycetes possess clamp connexions, which are accepted as homologous with the crosier hyphae occurring in the higher Ascomycetae, this group is regarded as being more nearly related to the Ascomycetae. The Heterobasidiomycetes are regarded as being derived from the Homobasidiomycetes.

The Homobasidiomycetes include most of the larger fungi such as the Mushrooms and Toadstools, the Puffballs and the Bracket fungi. They sometimes form conspicuous sclerotia and rhizomorphs. The basidia are arranged close together in a definite hymenium. They have no internal walls and bear externally, on sterigmata, a definite number of basidiospores. The mycelium of many species bears clamp connexions.

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There are two orders distinguished from each other by having the hymenium either exposed early or enclosed till after the basidiospores are mature.

Hymenomycetales—Basidia in hymenia which are exposed before the spores are mature.

Gasteromycetales—Basidia in hymenia which are enclosed till the spores are mature within a soft, gelatinous mass or gleba surrounded by a covering of sterile hyphae.

The Heterobasidiomycetes include the Jelly Fungi, the Rusts and the Smuts. The basidia are usually four-celled, except in the smuts. Each cell produces a single spore borne on the end of a sterigma.

Dacryomycetales—Basidia undivided below. This lower portion produces two widely divergent processes, each of which bears a single spore.

Tremellales—Basidia longitudinally divided into four cells each of which bears a spore. When the spores germinate they may give rise to conidia almost at once.

Auriculariales—Basidia transversely divided into four cells. Spores all borne about the same level on the hymenium due to differences in the length of their stalks.

Uredinales—These are the Rust Fungi and are obligate parasites on a wide range of vascular plants. Those members of the order which have a complete life cycle have five spore forms. Spermatia are produced in flask-shaped spermatogonia, aecidiospores in cup-like aecidia, uredospores and teleutospores in regular groups or beds (sori). The basidia, which arise from the teleutospores, are four-celled with transverse septa. Each cell produces a single basidiospore on a sterigma.

Ustilaginales—These are the Smut Fungi. They are parasites of higher plants, notably grasses. They produce spores in dense black, dusty masses. Each spore on germination gives out a short germ tube or promycelium, which functions as an irregular type of basidium. It may be septate or aseptate. Each cell gives a variable number of basidiospores which are either sessile or stalked. On germination these may bud off secondary spores.

BASIDIOMYCETAE— HOMOBASIDIOMYCETES

IN SPITE of the immense variety in the form of the fructifications occurring in this group, the general life histories have much in common. All the fungi have an undivided basidium. The young basidium contains a pair of nuclei derived from the division of the pair situated nearest to

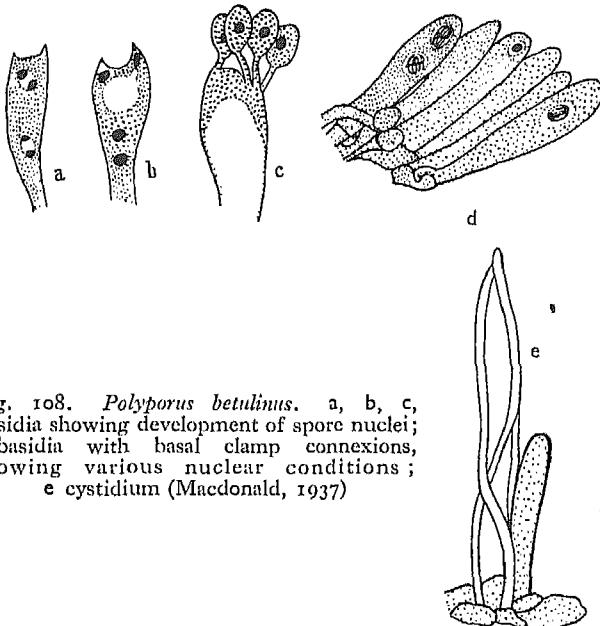


Fig. 108. *Polyporus betulinus*. a, b, c, Basidia showing development of spore nuclei; d basidia with basal clamp connexions, showing various nuclear conditions; e cystidium (Macdonald, 1937)

the slender hyphal tip which matures into the basidium. This division is associated with the formation of a clamp connexion (see pp. 9–10 and 102) and of cross walls cutting off the developing basidium from the rest of the hypha (Fig. 108d). The older basidium is uninucleate due to the fusion

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of the two members of the pair. The fusion nucleus divides reductionally to give the four haploid spore nuclei (Fig. 108a, b, c). There are exceptions to this, notably certain species of *Mycena*, where eight nuclei are formed. Four of these pass to the spores and the other four degenerate.

The basidia are formed on a hymenium which bears sporangia of all ages. They are interspersed with sterile hyphae, paraphyses, and, in some cases, with cystidia. These last are large structures which vary in shape but which usually have thick walls and apparently serve a mechanical function, helping to preserve the shape of the fruitbody and prevent crushing of the basidia (Fig. 108e).

The cells of the mycelium produced by a germinating basidiospore contain single nuclei. This mycelium does not, as a rule, persist for long. It corresponds to the haploid, vegetative mycelium of the Ascomycetae, but it does not bear sexual organs. However, only a comparatively small number of investigated Basidiomycetae can complete their life histories from a single spore. In most, two mycelia containing single (unpaired) nuclei must come together. Tips of branches anastomose and nuclear migration takes place, resulting in the formation of portions of hyphae containing paired nuclei, one member of each pair coming from each mycelium. The paired nuclei are said to form a dikaryon or heterokaryon. The latter name is to be preferred as indicating the different origin of the two members of each pair. The hyphae containing the heterokaryons grow strongly, producing a new mycelium of unlimited growth. This growth corresponds with the ascogenous hyphae; but, in the Basidiomycetae it constitutes a self-supporting mycelium of much greater permanence and importance than the haploid stage. Years may elapse before it bears basidia. The two nuclei of each heterokaryon always divide simultaneously and in most cases their division is associated with the formation of a clamp connexion (*see pp. 9-10*). This close association of the members of a pair continues until they fuse in the maturing basidium.

All those forms in which the life history cannot be

Basidiomycetae—Homobasidiomycetes

completed by the mycelium produced from a single spore are usually referred to as heterothallic. Groves (1951), however, regards this phenomenon not as heterothallism but as a mechanism for bringing about outbreeding, i.e. as homothallism with reciprocal fertility. In a few species of *Coprinus*, etc., there are four spore types. According to Groves, in these tetrapolar types there are two pairs of sterility factors involved.

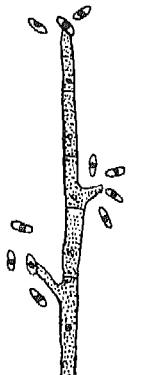


Fig. 109. *Typhula trifolii*.
Formation of uninucleate oidia
(after Noble, 1937)



Fig. 110. *Mycena sanguinolenta*.
Formation of binucleate oidia
(after Forsyth,
1950)

Additional reproductive methods, such as conidia on the primary mycelium, are not nearly as important here as in the Ascomycetae. Oidia sometimes occur on secondary mycelia as a result of fragmentation of the hyphae (Figs. 109, 110). Hyphae may be massed together to form sclerotia or structures of similar nature in wood attacked by the fungi, or they may form rhizomorphs.

HYMENOMYCETALES

In some members of this order, typified by the first family, there is no very definite fructification.

Exobasidiaceae—*Exobasidium vaccinii* (Fuckel) Wor. occurs as a parasite of *Vaccinium myrtillus* and *V. vitis-idaea*. A bright red colour is produced in infected leaves of the former plant and this is associated with a very upright type of growth. In the latter species distortion of the whole or of part of the leaves occurs (Fig. 111a). The swelling is due to the

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development in the spongy parenchyma of rounded or polygonal cells with no intercellular spaces.

The hyphae are intercellular with branched haustoria occurring within the host cells. The basidia are produced free on the leaf surface and cause a bloom as in *Taphrina* (Fig. 111b). The basidiospores, which vary in number within the genus from two to eight, may germinate to give mycelium or may produce curved conidia in a manner comparable with conidial production in *Taphrina* (Fig. 111c).

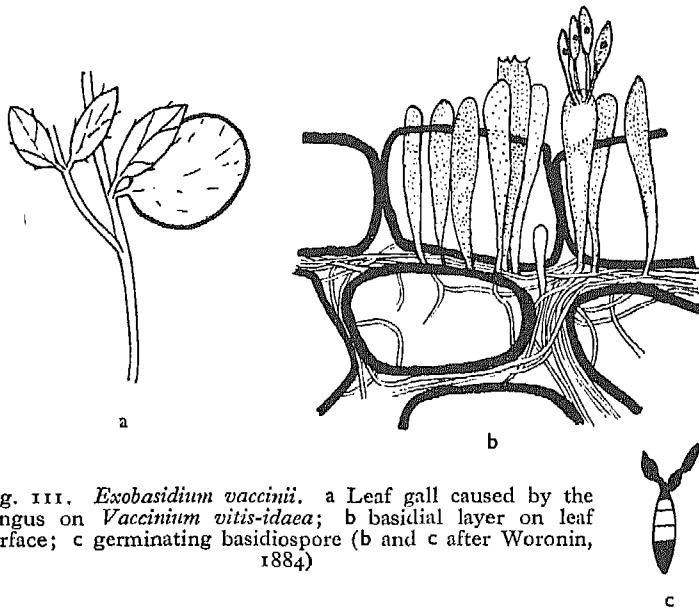


Fig. 111. *Exobasidium vaccinii*. a Leaf gall caused by the fungus on *Vaccinium vitis-idaea*; b basidial layer on leaf surface; c germinating basidiospore (b and c after Woronin, 1884)

In the great majority of the Hymenomycetales which constitute the Hymenomycetes of many authors, there is a hymenium of basidia and paraphyses (Fig. 112) covering the surface of a more or less well-developed fruitbody. In the least specialized types the hymenium is borne exposed on a flat surface. This is the resupinate type which occurs in species of *Stereum* (Fig. 113). In *Stereum hirsutum* Fr. there also occurs the bracket-like or dimidiate type of fructification (Fig. 114). The fruitbodies are attached laterally and the

Basidiomycetae—Homobasidiomycetes

hymenium is placed on the lower surface. It is more usual with dimidiate fructifications to find that the hymenium is not freely exposed but is arranged lining the surface of pores, as in *Polyporus* (Fig. 115). The most specialized fruitbody is that exemplified by the mushroom, *Psalliota*. In this type there is a central stipe or stalk surmounted by a cap or

Fig. 112. *Typhula gyrans*. Hymenial layer (Macdonald, 1934)

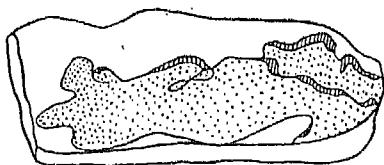
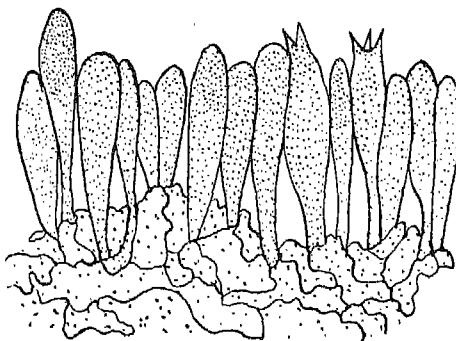


Fig. 113. *Stereum purpureum*. Resupinate fructification

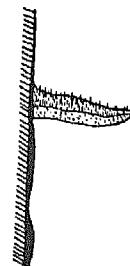


Fig. 114. *Stereum hirsutum*. Dimidiate fructification

pileus. The hymenium is produced lining the surface of radiating gills on the under-surface of the cap (Fig. 116). In addition to giving greater protection to the developing basidia, the positioning of the hymenium in gills or pores increases the fertile surface many times.

Thelephoraceae—In this family the hymenium is spread over a smooth or corrugated surface.

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Stereum hirsutum Fr. is a saprophyte or parasite on the wood of hardwood trees, especially oak. It produces a white rot. The sapwood is attacked first and later the heartwood also. Fructifications appear on the outside of attacked stems. Young ones are resupinate and the older ones dimidiate. The fruitbody contracts when dry so that the hymenium is hidden and the hairy sterile surface exposed. It returns to the normal condition on wetting (Fig. 117).

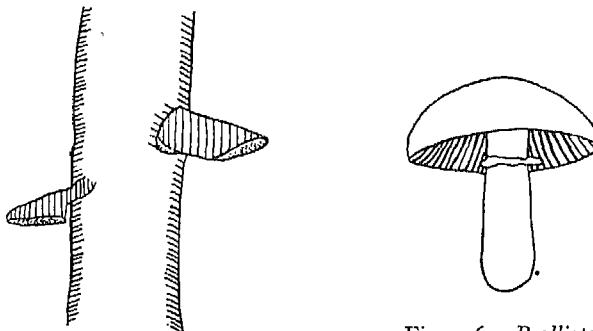


Fig. 115. *Polyporus betulinus*. Fruitbodies with upper, sterile surface and lower, fertile pore surface

Fig. 116. *Psalliota campestris*. Fruitbody with central stalk bearing cap with radiating gills on the under-surface

In this case, as in all examples of wood-destroying fungi dealt with later, damage can be kept at a minimum by the removal of all living or dead wood bearing the fructifications of the fungus, by careful pruning and by general attention to the health of the trees involved.

Stereum purpureum (Fr.) Fr. causes Silver Leaf Disease of a considerable range of tree and bush fruits. It is best known and most destructive on plums. Ultimately trees are killed outright. The bracket-like or resupinate fruitbodies (Fig. 118) are formed freely on branches after death, even while other parts of the tree are still growing. Young sporophores are purple in colour, older ones less brightly so. The basidia bear four oval, hyaline, thin-walled basidiospores, $5-7 \times 3-4 \mu$.

Basidiomycetae—Homobasidiomycetes

The first symptom of attack is the silvery appearance of the leaves. The presence of the fungus can be diagnosed by this before fructifications are produced. This is caused by the presence of air between the epidermis and the palisade layer, which have separated due to the action of toxic substances. These are produced by the hyphae of the fungus often several feet away down the stem.

Infection takes place through wounds in the stems. Wounds are least liable to attack when the carbohydrate

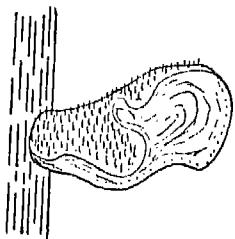


Fig. 117. *Stereum hirsutum*. Dimidiate fruitbody

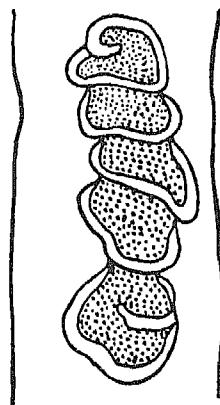


Fig. 118. *Stereum purpureum*. Resupinate fruitbodies on dead plum branch

content of the wood is low, i.e. during June, July and August. Accordingly, pruning should be carried out during these months, to minimize the danger of infection. The fungus often inhabits the dead wood of species to which it is not pathogenic. All such infected material should be collected and burned.

Polyporaceae—In this family the hymenium lines pores opening on to the surface of the fruitbody. This varies in shape from resupinate in *Merulius*, through bracket-like in *Polyporus* and *Fomes*, to pileate with a central stalk in *Boletus*.

Merulius lacrymans Fr. causes Dry Rot of woodwork in

Introduction to Mycology

buildings. This and other fungi associated with the decay of timber in buildings are dealt with fully by Cartwright and Findlay (1946). Humid conditions due to poor ventilation are the cause of outbreaks of Dry Rot. The fungus does not occur away from felled timber. Once established, the mycelium spreads rapidly. It grows in the wood elements. Slender hyphae pass through the walls of vessels, etc., delignifying them and causing the wood to undergo cubical cracking. It is this final stage which is described by the common name. After a while the mycelium comes to the surface on which it forms a thin, white, fan-like layer (Fig. 119a). Drops of water exude from the hyphae. These

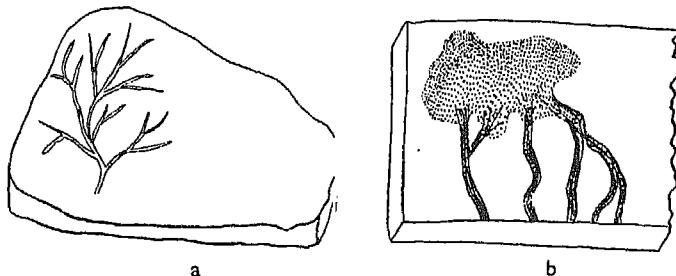


Fig. 119. *Merulius lacrymans*. a Fan-like mycelium on surface of attacked wood; b rhizomorphs on attacked wood surface

resemble tears and are responsible for the specific name of the organism. The surface mycelium forms string-like strands or rhizomorphs (Fig. 119b). These are capable of growing up to 6 feet through inorganic materials such as mortar, in order to reach and attack fresh pieces of timber.

The fruitbodies are mainly resupinate. They are pale grey at first and develop irregular, shallow pores. In these the basidia bearing the spores are produced. The latter are rusty red in the mass and very numerous. They colour the sporophore. Individually they are orange-yellow, elliptical and measure $9-10 \times 5-6 \mu$. They may appear as a red-brown powder near cracks on the surface of wood in buildings, thereby giving away the presence of the fungus behind the woodwork.

Basidiomycetidae—*Homobasidiomycetes*

To deal successfully with an attack of Dry Rot careful attention must be paid to the following points: the removal of all sources of dampness, especially an improvement of the ventilation system, careful eradication of all infected timber, the reduction of new timber to a minimum round the infected area, the sterilization of all contaminated inorganic materials and the treatment of all replacement timber with a fungicide.

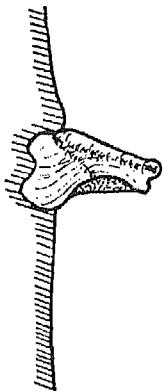


Fig. 120. *Polyporus betulinus*. Fruit-body on birch trunk

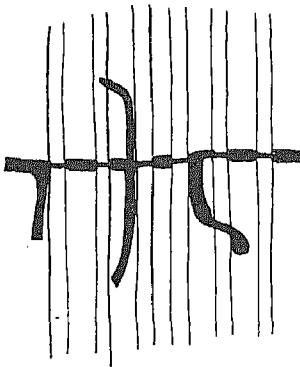


Fig. 121. *Fomes fomentarius*. Hyphae penetrating vessels in birch wood (Macdonald, 1938)

Polyporus squamosus Fr. frequently occurs in Britain as a wound parasite of elm and sycamore. It causes a serious heart rot of the branches of elm, ultimately bringing about the death of the tree. Its fructifications are annual, bracket-like, up to 65 cm. across. They are brown above and pale cream below. There is a short lateral stalk which may carry two or three fruitbodies. These have deep regular pores. The spore output is enormous; it has been estimated that a single sporophore may produce a hundred billion spores. When spore production is at its peak, a visible spore cloud may be formed. The spores are oblong and 10-12 × 4-5 μ .

P. betulinus Fr. is a very common wound parasite of

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birch in Britain (Fig. 120). It is an excellent indicator of the degree of neglect from which this tree suffers. Hyphae penetrate the vessels in both heartwood and sapwood, causing a cubical rot (Fig. 122). In the Highlands of Scotland it is often replaced by *Fomes fomentarius* (Fr.) Kickx (Fig. 121).

The fruitbodies in the genus *Fomes* are perennial, with regular, small pores. Sometimes, as in *F. fomentarius*, they

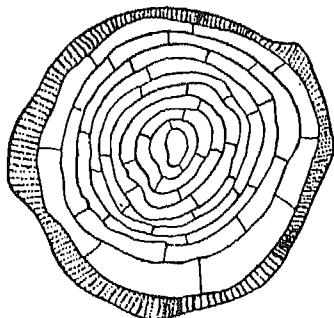


Fig. 122. *Polyporus betulinus*.
Cubical rot of birch wood

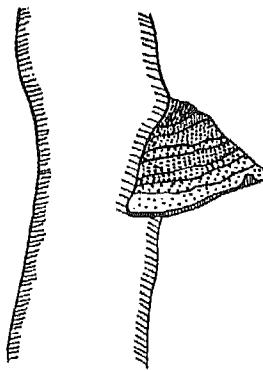


Fig. 123. *Fomes fomen-*
tarius. Fruitbody on
birch trunk

are hoof-shaped, producing a new layer of pores each year (Fig. 123). Their age can then be estimated by counting the number of pore layers.

Fomes annosus Fr. causes a root-rot and heart-rot of many forest trees. It is often destructive to pines in Britain. The fungus grows on the roots of a wide variety of trees and even shrubs such as *Ulex europaeus* L. and the bracken fern *Pteridium aquilinum* (L.) Kuhn. (Risbeth, 1950). From this infected material it is able to attack pine roots which come in contact with the mycelium during growth. To a limited extent the fungus may grow as a saprophyte in the soil, or on dead pieces of roots. In the latter case the extent and vigour of the mycelium seems to be governed by the presence of other wood-rotting saprophytes. If they are abundant,

Basidiomycetae—*Homobasidiomycetes*

Fomes annosus is suppressed. Pines planted on old woodland sites are liable to become heavily infected due to the abundance of infected material in the soil. Risbeth (1951) estimated that the mycelium spreads about 1 metre a year in the stump roots of felled trees. By this means it closely approaches standing trees within a year of the thinning of a plantation and is thus a dangerous source of new infections. In any woodland, conditions liable to induce root injury open the way for attacks by *Fomes annosus*. Even badly attacked pines may appear perfectly healthy when the heartwood is already rotted away for a number of feet at the base of the trunk.

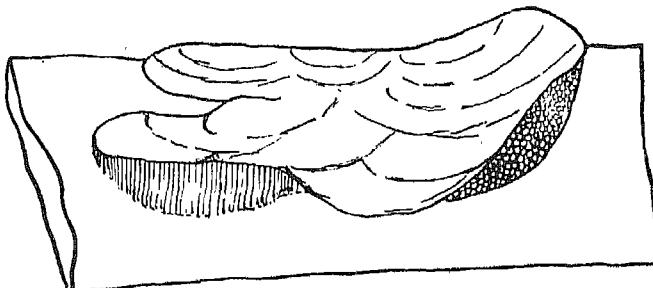


Fig. 124. *Fomes annosus*. Thin fruitbody on pine root.
Section of pore layer on left, surface view on right

The fructifications (Fig. 124) are thinner and more irregular than those of *Fomes fomentarius*. They are dark brown with a yellow pore surface. The spores are sub-globose, white, $4-5 \times 4 \mu$. Fruitbodies measuring 7-45 cm. across are formed about ground level. They may be more or less buried. They may be seen at the mouths of rabbit burrows and in the hollows associated with exposed roots.

Agaricaceae—Included in this family are all those species in which the fruitbody consists of a pileus and stipe and in which the hymenium is spread over the surface of radiating gills or lamellae on the under-surface of the head. The free ends of the hyphae which develop into the basidia and paraphyses stand at right angles to the rest of the hyphae which follow a longitudinal course in the middle part

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(trama) of the gill. The fruitbody may at first be covered by a thin veil of mycelium. As the stipe lengthens and the pileus expands this universal veil ruptures. In those species in which it occurs it remains visible in the adult fruitbody as a cup or volva at the foot of the stalk, and pieces of it may be seen adhering to the upper surface of the cap. In addition, in the young stage, the edges of the gills lie near to the stipe and may be connected to it by a second, partial veil. This covers the gills below until the pileus expands. Then it, too, ruptures to expose the hymenium; but the remains can be seen as a ring, the annulus, round the stipe (Fig. 125). In the genus *Amanita* both ring and volva are present.

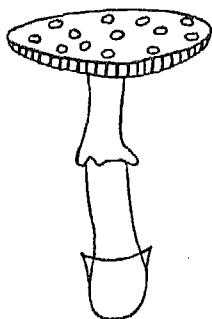


Fig. 125. *Amanita muscaria*. Fruit-body showing ring and volva

There is a large number of genera distinguished from each other by characters such as spore colour, and the presence or absence of annulus and volva. Most species produce large quantities of spores the colour of which can be determined by placing pilei on sheets of glass or white paper so that spore casts are obtained. The spores are shot off from the sterigmata with the correct strength to cause them to fall freely between the gills.

Psalliota campestris Fr., the common mushroom, is the only edible species which is grown commercially in Britain. In it there is an annulus present; but no volva (Fig. 116). The wild form has four-spored basidia and that most commonly cultivated two-spored basidia. The spores are purple-brown, $5.5-9 \times 5-7 \mu$.

Cultivated mushroom beds are established by planting "spawn" in the carefully prepared bed, the essential ingredient of which is dung. The exact composition of the "spawn" varies according to the method employed in its preparation; but it always contains the mycelium of the mushroom. Hyphae are inoculated into and allowed to

Basidiomycetae—Homobasidiomycetes

“run” through organic material, such as sterilized horse dung, until this material is permeated by the mycelium. The beds are “spawned” with this mixture. Some days afterwards, when the mycelium from the spawn has started to “run” through the dung, the bed is cased with soil.

Coprinus comatus Fr., Shaggy Caps, is a black-spored species (Fig. 126). It forms silky fructifications nearly 30 cm. in height on ground containing large amounts of organic matter. The ring is fugacious. The basidia are interspersed with large cystidia which hold the gills apart. The spores are $11-13 \times 6-7 \mu$. The main interest of the species is that it exhibits the phenomenon of autodigestion. The pileus is campanulate. The basidiospores mature progressively upwards from the rim of the pileus. After they are discharged the gills which bore them are converted to an inky liquid. This prevents the lower tissues from interfering with the discharge of the spores from the upper, inner portions of the gills where they mature later.

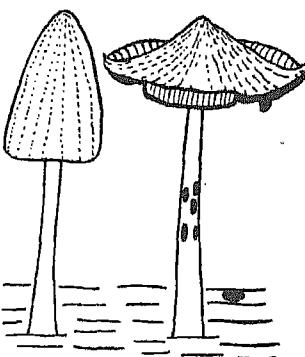


Fig. 126. *Coprinus comatus*.
Fruitbodies on soil. That on
the right shows autodigestion

Armillaria mellea (Fr.) Quél., the Shoe String fungus, is one of the best known species. It is a dangerous parasite of a wide range of coniferous and hardwood trees, shrubs and even herbaceous plants. Long after infection takes place, and frequently after the death of the host, groups of fructifications are formed at ground level at the base of the infected plant (Fig. 127). The tawny or honey-coloured pileus is 5-10 cm. across. The stem is tawny with a whitish ring, the gills are white as are the spores which measure $8-9 \times 5-6 \mu$. The mycelial strands are highly specialized to form rhizomorphs. These show three distinct regions in cross section. There is a limiting rind composed of thick-walled portions of hyphae. This portion is black in colour

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and may become mucilaginous in the mature rhizomorph. Inside it there is a densely interwoven mass of white hyphae forming a "cortex" and, in the middle, more loosely organized hyphae forming a "pith" (Fig. 128). This last region is often more or less hollow and supplies a means of aeration for the growing parts. There is a definite apical growing region. Rhizomorphs branch freely. Rhizomorphs in active growth are luminous. This is said to be due to auto-oxidation.

Rhizomorphs pass freely through the soil. They attack their hosts through the roots. Entry is gained through

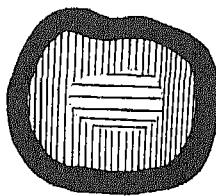
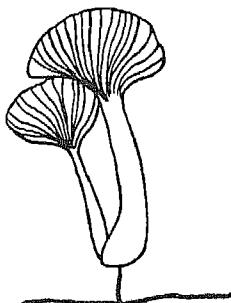


Fig. 128. *Marasmius androsaceus*. Section of a rhizomorph to show rind, cortex and pith (Macdonald, 1949)

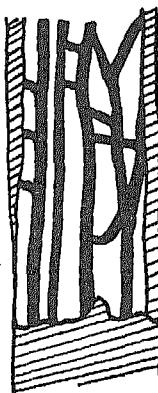
Fig. 127. *Armillaria mellea*. Toad-stools formed on rhizomorphous mycelium (adapted from Hiley, 1919)

wounds, at the origin of lateral branches, or even by uninjured tissues. Penetration of the stem through the bark at ground level also occurs. An infected tree is killed from the roots upwards. Once the bark is penetrated, the fungus forms a white mycelial plate in the position of the wood cambium. This is followed by the formation of flattened, anastomosing rhizomorphs. The rhizomorphs spread up the stem in this position, tending to separate the bark from the wood (Fig. 129). Hyphae penetrate the wood, spreading chiefly by means of the medullary rays, but attacking the lignified elements. Pseudo-sclerotia are formed in the infected tissues.

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It is probable that there are races of the fungus showing varying degrees of parasitism. The fungus requires the presence of a good deal of moisture to grow successfully. It frequently causes damage where trees are growing under swampy conditions. Any factor upsetting the normal growth, such as defoliation by insects, seems to render trees more susceptible to attack. The fact that the fungus flourishes as a saprophyte renders its control difficult; but the removal of dead stumps reduces centres of infection. Ring barking of trees some time before felling has been used in order to

Fig. 129. *Armillaria mellea*. Infected birch stem, bark removed to expose rhizomorphs



deprive any fungus mycelium in the roots of its source of manufactured food and thereby starve it out.

GASTEROMYCTALES

This order of fungi was at one time regarded as forming a parallel development series to the Hymenomycetales. It is most probable, however, that the species are polyphyletic and that, when a natural grouping becomes possible, it will show that they can be arranged along several lines of development. There are certain features common to the group. They have closed basidiocarps, *i.e.* until the spores are mature, the hymenium is enclosed within a continuous membrane or peridium. This consists of one or more layers. Contained within this membrane are the spore-bearing

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tissue or gleba and sterile tissue (Fig. 130a). The basidia are variously arranged. In the young stage the gleba may contain scattered groups of basidia, or produce a number of hymenia enclosed in separate little structures termed peridiola, or be traversed by a definite hymenial tissue borne on irregular plates which form variously-shaped cavities. As the basidia are enclosed, they have lost their function of securing spore dispersal. The basidiospores are no longer forcibly discharged. Their dispersal is secured with the help of wind, large animals or insects.

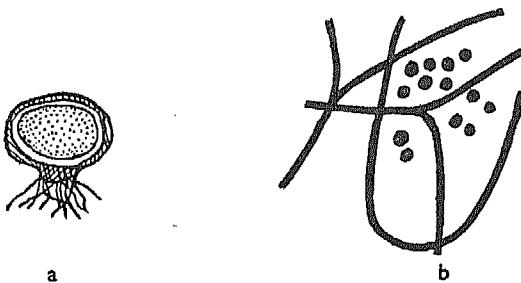


Fig. 130. Gasteromycete. a Diagrammatic drawing of section through fruitbody to show spore-bearing tissue surrounded by sterile membrane; b spores and capillitium

In some species the development of the fruitbody is entirely hypogaeous, in others entirely epigaeous. In many, part of the development takes place below ground but it is completed above ground. The hypogaeous species are naturally the least well known and there may be many awaiting discovery and investigation. A pointer to this is given by the fact that Hawker (1951) collected 12 hypogaeous basidiomycete fungi, during the course of a year, in beech woods or under evergreen oaks, chiefly in the west of England.

The glebal tissue in many species disintegrates at maturity so that only a powdery mass of spores remains. In some genera, however, certain hyphae persist, forming thick-walled, simple or branched structures. They constitute a capillitium functioning in connexion with spore dispersal

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as in many typical Puffballs (Fig. 130b). There may be a sterile axial portion, the columella forming a short stipe as in *Lycoperdon* (Fig. 131) or elongating very considerably as in *Ithyphallus* (Fig. 132).

The vegetative mycelium in most Gasteromycetales is organized into cord-like or rhizomorph-like strands. The fructifications arise on these.

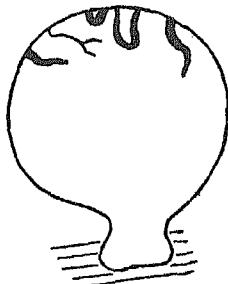


Fig. 131. *Lycoperdon*.
Fruitbody with short
stalk

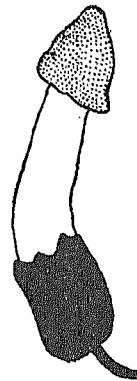


Fig. 132. *Ithyphallus*. Fruitbody with
much elongated
stalk

Classification depends on the position of the basidia. The species are usually divided into about half a dozen groups. The following examples are representative of three very distinct types.

Lycoperdaceae—The genera *Lycoperdon*, which contains the common Puffballs, *Bovista*, the small Puffballs, and *Geaster*, the Earth Stars, belong to this family. All occur mainly in pastures. They are edible when young.

In *Lycoperdon* there is a double layered peridium, the outer layer often being roughened and scaly, as in *L. gemmatum* Batsch. In *Geaster* the peridium is three-layered. The two outer layers forming the exoperidium, which splits from above downwards into a number of lobes, creating a star-like effect (Fig. 133).

The basidia are irregularly scattered in groups throughout

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the fructification. The hymenium may surround a number of small chambers formed by irregular growth causing tearing of the internal tissues. There is a capillitium of thick-walled, brown hyphae. This aids in the opening of the inner layer of the peridium. The spores are dry and dusty and are frequently distributed by wind. The actual expulsion may be brought about by pressure on the sides of the fruit-body caused by animals. Spores may also be washed out of the fructification by rain during wet weather. In *Bovista* there is no sterile basal portion. This is present in *Lycoperdon* (Fig. 134). It is developed into a conspicuous stalk in

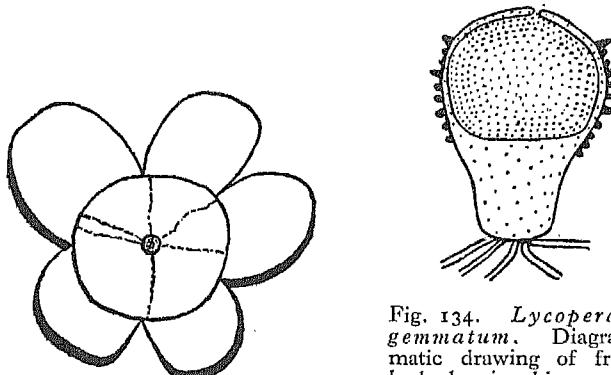


Fig. 133. *Geaster*. Earth Star fruitbody with exoperidium split open

Fig. 134. *Lycoperdon gemmatum*. Diagrammatic drawing of fruit-body showing rhizomorph-like mycelium, sterile basal and fertile upper parts. Dehiscence by an apical pore

L. gemmatum. In this species the puffball is roughly 7×10 cm. in size and opens by an apical pore. The spores are about 4μ in diameter. It is found from July to November.

Nidulariaceae—This family contains the Birds' Nest fungi. The fructifications measure a few millimetres only. The gleba is broken up into a number of separate indehiscent peridiola enclosed in the peridium, which breaks open at the apex to expose a cup containing a number of separate discs (Fig. 135a). Inside each peridiolum is a hymenium lining a central cavity (Fig. 135b).

Crucibulum vulgare Tul. occurs on decaying wood. Its

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fructifications are brown to grey in colour, oval in shape, and measure $3\text{--}7 \times 4\text{--}8$ mm. There is a two-layered peridium. The outer layer is thick and felty and the inner layer thin and membranous. There are about six chambers inside. Round each is a thick-walled dark tissue which forms the wall of the peridiolum. The other tissues inside the peridium break down and become gelatinous. The peridiola are lenticular in shape and $1\text{--}2$ mm. in diameter. Each is attached to the wall of the peridium by a cord, the funiculus, composed of long, thick-walled, hyaline hyphae (Fig. 135c). The peridium breaks down as do the funiculi and the peridiola are set free. They are probably scattered

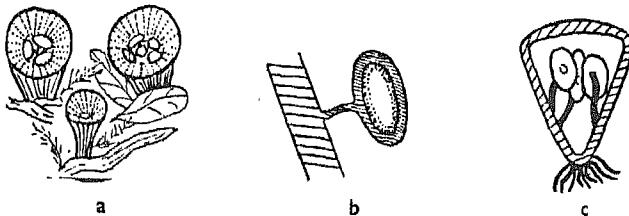


Fig. 135. *Crucibulum vulgare*. a Mature fructifications with peridiola exposed; b section of single peridiolum with internal hymenium ; c peridiola with funiculi

by the splashing of rain drops. They have no definite opening and the basidiospores are set free only after decay of the peridiola. The spores are hyaline, elliptical and vary considerably in size, $3\cdot5\text{--}5\cdot5 \times 4\cdot3\text{--}8\cdot6 \mu$. There are 2-4 spores per basidium and they are borne on slender sterigmata.

Brodie (1951) has reported that investigated species belonging to the four different genera of the Nidulariaceae all show tetrapolar (four-mating-type) heterothallism. He has found also, in *Crucibulum*, that in "mating" certain pairs of haploid mycelia, nuclei pass from one haploid to the other and not in both directions so that there are "donor" and "acceptor" mycelia. This is opposed to the condition normally described as occurring in Basidiomycetae in which nuclear movement takes place in both directions at "mating" so that both haploid mycelia come to contain heterokaryotic pairs of nuclei.

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Phallaceae—This family contains the Stinkhorn Fungi. The gleba is raised on a stalk. The mature spores are embedded in mucilage. The fructifications smell like carrion and attract insects which mechanically distribute the spores.

In *Ithyphallus impudicus* Fr. the fructifications in the early stages are usually more or less concealed in the surface humus of soils containing decaying wood. They are borne at the tips of white, subterranean mycelial cords. At first the fructification is rounded. It may grow to be the size of a hen's egg (Fig. 136a). The peridium then ruptures and part of the internal tissue elongates to form a stalk which bears the gleba at the top as an olive-green mucilaginous

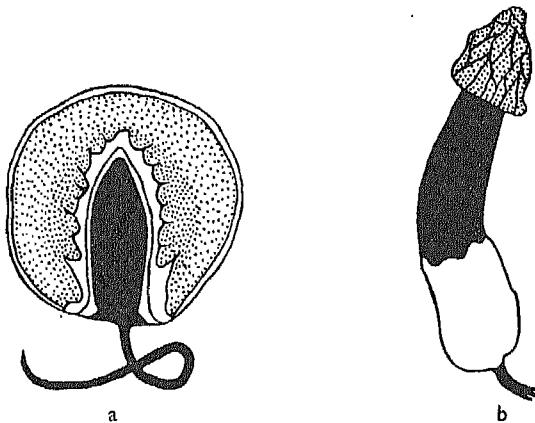


Fig. 136. *Ithyphallus impudicus*. a Young fructification on mycelial cord; b mature fructification with extended stalk and apical gleba

mass or cap. The cap is reticulated outside and attached only at the apex. The fruitbodies are up to 16 cm. high when mature. There is a volva round the base of the stalk (Fig. 136b). The full size of the fructification is attained in a few hours after the bursting of the volva. The plants may be found from May to November, usually under trees. The basidia are embedded in the mucilage. They bear four spores each; these average approximately $1.6 \times 3.5 \mu$.

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IN THIS group the basidia are septate or deeply cleft. In most of the orders, they are four-celled, each cell producing a single spore on the end of a sterigma.

DACRYOMYCETALES

These fungi suggest a link between the Homobasidiomycetes and more typically heterobasidiomycetous forms. *Dacryomyces deliquescent* Duby, a member of the Dacryomycetaceae, is a saprophyte growing on dead wood, under

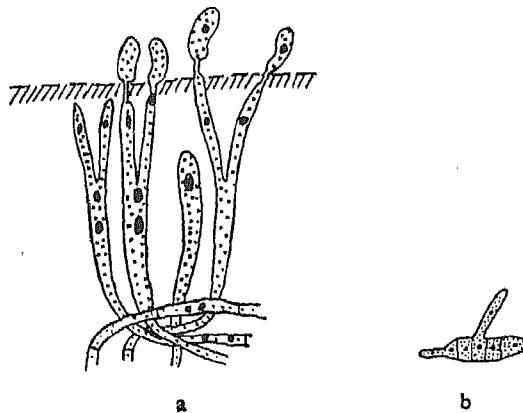


Fig. 137. *Dacryomyces deliquescent*. a Diagrammatic drawing of part of hymenium with basidia and spores; b germinating basidiospores

damp conditions. The fructifications are small, up to 3 or 4 mm. across, but usually confluent. They are bright orange in colour to begin with and bud off binucleate conidia. These are irregular, resembling terminal cells of the mycelium. Each divides before germination into two

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uninucleate parts. Each portion may give a mycelium of uninucleate cells. Later, the fructification becomes firmer and yellow. It now bears a somewhat irregularly wrinkled hymenium. This consists of Y-shaped, non-septate, but

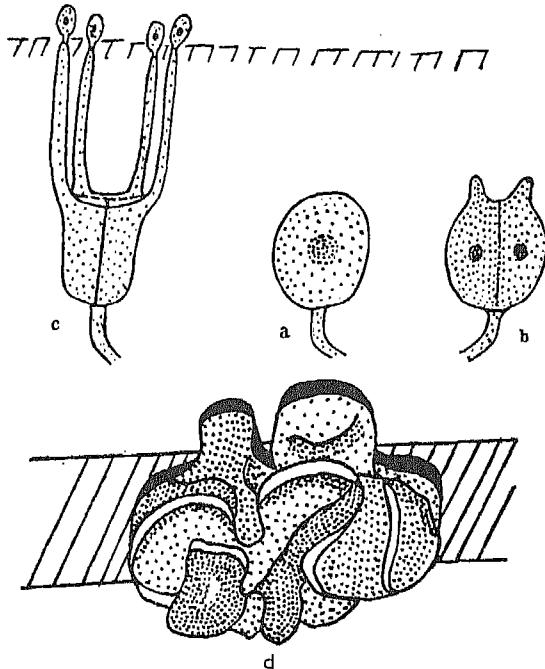


Fig. 138. *Tremella mesenterica*. Diagrammatic drawing of section of fruitbody. a Young hypobasidium; b older stage with four cells separated off by vertical divisions; c mature stage with 4 epibasidia, sterigmata and spores; d gelatinous fruitbody

deeply cleft basidia (Fig. 137a). The lower portion is sometimes called the hypobasidium and the two arms the epibasidia. Four nuclei are formed in the basidium in the usual way, but two remain in the hypobasidium or one in each epibasidium, while the other two pass to the two spores (Fig. 137a). The basidiospores are white, cylindrical and curved, $8-22 \times 4-7 \mu$. They are non-septate and

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uninucleate when shed. They become divided by septa into a number of uninucleate parts. Each part may germinate by a germ tube (Fig. 137b).

TREMELLALES

In this order the basidia are longitudinally divided into four cells, so that they appear cruciate when seen from above. In the Tremellaceae, *Tremella mesenterica* Fr. has a bright orange fruitbody which forms on dead branches and

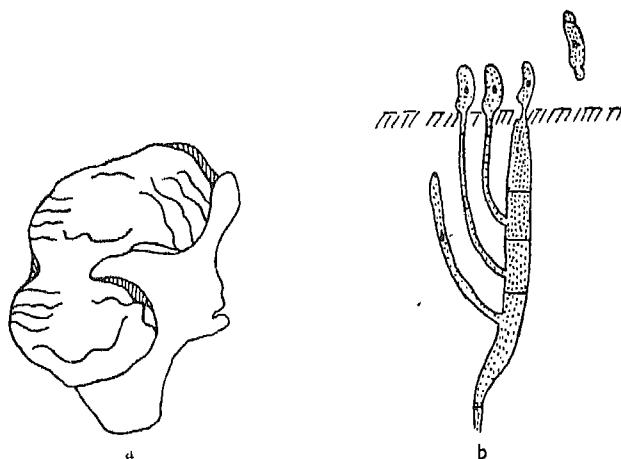


Fig. 139. *Auricularia auricula-judae*. a Fructification from elder stem; b diagrammatic drawing of mature basidium showing transversely-septate hypobasidium, 4 epibasidia with sterigmata of unequal length and spores

twigs. It also is gelatinous when young, though old fruitbodies are firm and tough. It is much contorted and resembles the appearance of a brain (Fig. 138d). It is up to 7 cm. in diameter. The hypobasidium is longitudinally divided into four uninucleate cells, from each of which arises a long stalk, the epibasidium, projecting to the surface of the jelly and bearing a basidiospore (Fig. 138a, b, c). The spores are white, elliptical, uninucleate, $13-14 \times 7-8 \mu$.

AURICULARIALES

In the Auriculariales the basidia are transversely divided. *Auricularia auricula-judae* Schroet., the Jew's Ear fungus, belonging to the Auriculariaceae, is typical of this order. This fungus appears all the year round, but more especially in winter, on branches of many trees, particularly elder. It grows as a saprophyte or as a weak parasite. It forms fructifications up to 8 cm. in diameter. They are grey, then brown and finally black in colour. They are gelatinous when young, becoming cartilaginous and tough when old. When mature they are somewhat ear-shaped with a folded hymenium on the upper surface (Fig. 139a).

The basidium consists of a hypobasidium transversely divided into four cells. Each cell produces a single spore. All the spores come to lie about the same level on the hymenial surface due to the different lengths of their stalks or epibasidia (Fig. 139b). The spores give a grey bloom to the surface. They are white, oblong or cylindrical, curved, $16-20 \times 6-9 \mu$. The spores either germinate by means of a germ tube or produce groups of curved conidia. The cells of the ordinary mycelium are heterokaryotic. Fusion of the nuclei occurs in the developing hypobasidium. The spores are uninucleate. Where the heterokaryon is initiated is not known.

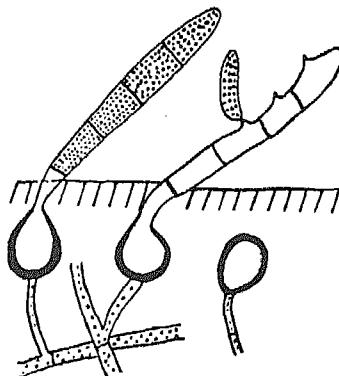
This type of basidium resembles that which occurs in the Uredinales in having transverse septa. The basidia in the related genus *Septobasidium* are, in certain species such as *S. pseudopedicellatum* Burt., more like those of the Uredinales. The hymenium here bears ovoid cells which become thick-walled. Each of these is called a probasidium and corresponds with the teleutospore in the Uredinales. When the probasidium germinates it produces an elongated tube which becomes divided transversely into four cells. This structure corresponds with the hypobasidium. Each of its cells produces a very short stalk or epibasidium, on the end of which a basidiospore is produced (Fig. 140). The basidiospore becomes divided into about eight cells before it is set

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free. Each cell may germinate by a germ tube or bud off conidia. The vegetative hyphae do not produce clamp connexions.

The genus *Septobasidium* is of interest also because certain of its species have a symbiotic relationship with scale insects. The mycelium of the fungus forms patches on the bark of trees in tropical and warm temperate parts of the world. The insects shelter beneath the stroma and some of the hyphae grow into their bodies through the external openings. This may have fatal results; but enough insects survive

Fig. 140. *Septobasidium pseudopedicellatum*. Probasidia, basidia and spores (adapted from Couch, 1938)



long enough for reproduction to take place so that the relationship is a permanent one. Fungus and insect combine to cause cracking of the tree bark and injury to the host.

UREDINALES

The best-known of the 5,000 to 6,000 rust fungi is *Puccinia graminis* Pers., Black Rust of wheat and other cereals. It belongs to the family Pucciniaceae. It is a fungus of great economic importance. It causes losses in the yield of wheat which have been estimated at 50 per cent in years in which the attack is very severe. The fungus illustrates the diversity of spore forms occurring in the order and the phenomena of heterothallism, physiological specialization and heteroecism. This last is the use by a fungus of more than one species of host plant in order to complete its life history.

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The thick-walled, resting spores, which correspond with the probasidia of the Auriculariales, are the teleutospores. The number of cells varies between genera from one in *Uromyces* (Fig. 141) to many in *Phragmidium* (Fig. 142). In *Puccinia* they are two-celled; the teleutospores of *Puccinia graminis* measure $40-60 \times 15-20 \mu$, each cell contains a single, diploid nucleus (Fig. 144a). The teleutospores are produced



Fig. 141. *Uromyces*.
One-celled teleuto-
spore



Fig. 142. *Phragmid-
ium*. Four-celled
teleutospore



Fig. 143. *Puccinia
graminis*. Teleuto-
spori on leaf sheath
of wheat

in elongated sori which are black in colour and appear mainly on the stems and leaf sheaths of the affected cereal. The sori break through the epidermis in early autumn (Fig. 143). In spring, each cell of the teleutospore germinates with the production of a basidium which resembles a germ tube. The germ pore is at the apex in the upper cell and, in the lower cell, just below the transverse septum. The basidium is divided by transverse walls into four cells. The diploid nucleus by reductional division gives four haploid nuclei, one for each cell. Each cell produces one basidiospore on a sterigma and a single nucleus passes to each spore (Fig. 144b). The basidiospores are carried by wind to developing leaves of *Berberis vulgaris*, the barberry. The cuticle of the barberry leaves is thin at this time and the

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germ tube developed from the basidiospore is able to penetrate the surface by pressure. Once inside, the hyphae spread between the cells of the leaf and form irregular haustoria penetrating the host cells. The mycelium thus formed is haploid. Its cells contain single nuclei. Affected parts of leaves are thickened and develop a red colour due to the breakdown of the chlorophyll. In the infected areas two other types of spore-bearing organ are produced. First,

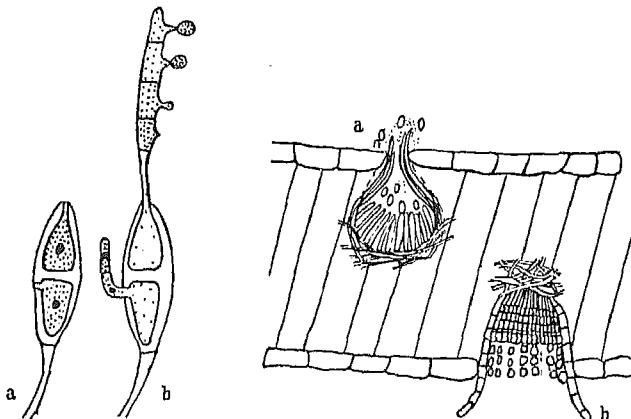


Fig. 144. *Puccinia graminis*. a Mature teleutospore; b formation of transversely-septate basidium with spores

Fig. 145. *Puccinia graminis*. Diagrammatic drawing of berry leaf section, with a spermatogonium opening on the upper surface and b aecidium opening on the lower surface

toward the upper side of the leaf, little flask-shaped spermatogonia appear embedded in the tissues, but with their ostioles projecting to the upper surface. Within the flasks large numbers of minute spermatia are budded off from the ends of the hyphae (Fig. 145a). Each contains a relatively large nucleus with a very little cytoplasm. Meanwhile, towards the lower surface, cup-shaped accidia are developing (Figs. 145b, 146). The hyphae forming them are also uninucleate and haploid. If they remain so, the aecidium does not produce accidiospores. The spermatia are exuded

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at the ostiole of the spermogonium mixed with a sweetish nectar. They are mechanically transferred from one spermogonium to another by insects and so reach special hyphae which emerge from the leaf surface near or within the spermogonia (Fig. 147). These emergent hyphae connect with the aecidial initials below. Following on this fusion, the aecidium produces binucleate aecidiospores in many parallel chains (Fig. 148). The spores are 14–26 μ in diameter.

The implications of these phenomena are twofold: First, that the haploid nucleus in the spermatium is a male



Fig. 146. *Puccinia graminis*. Surface view of barberry leaf with cluster of aecidial cups



Fig. 147. *Uromyces scirpi*. Spermatium fused to receptive hypha (after Fort, 1940)



Fig. 148. *Puccinia graminis*. Chain of binucleate aecidiospores

nucleus and that it or its descendants reach the aecidial initials and fertilize the haploid, female cells, this fertilization being followed by the production of chains of aecidiospores in which the male and female haploid nuclei are associated to form the beginning of the heterokaryotic phase in the life history of the fungus; secondly, that the haploid thallus of the rust is homothallic, as it bears both spermogonia and aecidia, but self-sterile, as the heterokaryon is not initiated unless nuclei contained in spermatia from another thallus, i.e. originating from an infection caused by another basidiospore, are brought into association with the nuclei of the aecidial initials. This is the view adopted by Groves (1951),

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who regards this phenomenon here and in the Hymenomycetales as a mechanism for bringing about outbreeding.

The mature accidium contains chains of binucleate aecidiospores which are orange in colour due to the presence of oil droplets. The cup has a limiting layer or pseudo-peridium which projects through the lower epidermis and has back-turned edges (Fig. 145b). The mature aecidiospores are carried by air to the cereal plant. Here each germinates by production of a germ tube which enters the host through a stoma pore. Infection is most severe on the leaf sheaths, though it also occurs on stems and on leaf

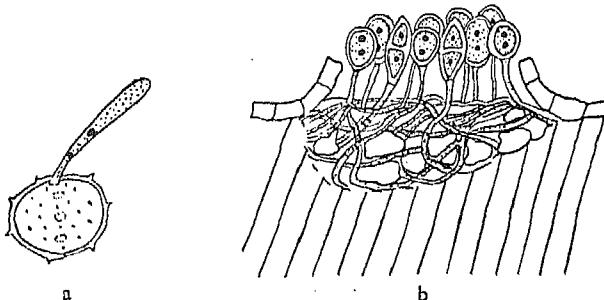


Fig. 149. *Puccinia graminis*. a Uredospore showing binucleate germ tube and four equatorial germ pores; b section through sorus on leaf sheath of wheat. Both uredospores and teleutospores are present

blades. The hyphae are intercellular with rounded or irregular haustoria. During summer the mycelium produced gives rise to sori containing single-celled, binucleate uredospores, measuring $25-30 \times 17-20 \mu$. They are oval in shape with a thick, prickly wall in which there are four equatorial germ pores (Fig. 149a). The spores are rusty coloured in the mass and it is profuse spore production at this stage which causes the fungi to be called rusts. The uredospores are readily carried by air currents and are a means of vegetative reproduction by which the rust is spread over wide areas. The spores have been gathered in a viable condition at heights up to 10,000 feet.

The uredospores germinate through one or other of the

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germ pores. The germ tubes produced repeating the same type of infection on the cereal host. Later on in the season, teleutospores appear in the same (Fig. 149b) or in different sori. The sori are often longer and are much darker in colour. The delayed fusion of the paired nuclei takes place in the developing teleutospore (Fig. 149b). As the reduction division takes place at its germination, the teleutospore is the only truly diploid stage in the life history of the rust.

Puccinia graminis has the life history of a typical heteroecious rust. There are two phases in its life cycle, each passed on a different, not closely related, host plant. There are other rusts such as *P. menthae* Pers., the Mint rust, in which all the spore forms are produced on the one type of host, *i.e.* which are autoecious. There are many with one or other of the spore forms lacking and *P. malvacearum* Mont., the Hollyhock rust, produces teleutospores only. In *P. malvacearum* the doubling of the nuclei takes place just before teleutospore formation so that the greater part of the mycelium is haploid and uninucleate.

Physiological specialization of races is common among species of rusts. It is well seen in *Puccinia graminis*. The fungus is first of all divided into a number of host-species. Thus *P. graminis tritici* occurs on wheat and *P. graminis avenae* on oats and some other grasses. In addition, within each host-species there are races which differ from each other in the type of symptoms they produce on a particular variety of the host species. There are over 200 known physiological races of *P. graminis tritici*.

The number of physiological races occurring in countries where the alternate barberry host is absent is much smaller than in those in which it is present. In Australia the passage of a race of *P. g. tritici* through the barberry host was followed by the appearance of a strain new to Australia. This and other examples lead to the conclusion that these rusts have the faculty to produce, by segregation, new physiological races. As such new races may be dangerous parasites, this is a forcible argument in favour of the eradication of the barberry alternate host.

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Barberry eradication was carried on both in Europe and in America before the question of physiological specialization arose. It was designed simply to break the life cycle of the fungus with a view to causing it to die out. This it did not do due to the ability of the fungus to survive by means of uredospores in favourable areas and re-enter by the same means those areas from which the temporary severity of the climate had excluded it. The measure did, however, reduce the incidence of the disease and must have prevented the appearance of new, more actively-pathogenic races.

Pioneer work by Biffen (1907) showed that the inheritance of resistance or susceptibility in wheats to the strain of yellow rust, *Puccinia glumarum* (Schlm.) Erickss. and Henn., with which he was working followed a simple Mendelian ratio for single factor dominance of susceptibility. He was, therefore, able to breed resistant races of wheat. The picture is not usually so easy to understand. Most work has been done on *P. g. tritici* in America. It has been shown that there may be one or more factors involved and that these may be inherited either as dominants or recessives. It has been found possible to breed wheat varieties commercially suitable for particular regions which are resistant to the races of the rust most widespread in the area. However, the introduction of another race of the rust to which the new wheats are not resistant may make it necessary to start breeding work again.

USTILAGINALES

The Ustilaginales or Smut fungi are parasites of flowering plants. The British members of the families Ustilaginaceæ and Tilletiaceæ have been described by Ainsworth and Sampson (1950).

The thick-walled resting spores, chlamydospores, of the Ustilaginales correspond with the teleutospores of the Uredinales and with the probasidia of the Auriculariales both in their function and in the position which they occupy in the life history of the fungus. The resting spores are black and form the sooty masses which have caused

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these fungi to be termed Smuts. Usually, breakdown and death of tissues occur only in the part of the host occupied by the sorus which contains the chlamydospores. The mycelium ramifies elsewhere, but it is normally confined to one type of organ in the case of any particular species. It is largely intercellular, forming haustoria inside the host cells, though it is intracellular in *Ustilago maydis* (DC.) Corda. There seems to be a state of equilibrium held between the host and the mycelium of the parasite.

The smuts were for long supposed to be obligate parasites; but it is now known that the spores will germinate in culture

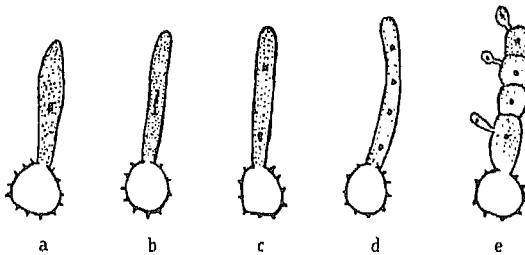


Fig. 150. *Ustilago*. Development of transversely-septate basidium from a thick-walled chlamydospore. The nucleus in each cell divides at spore production (Smith, G. M., 1948, by courtesy of McGraw-Hill Book Co. Inc.)

media and the resulting mycelia grow thereon. This means that there is a possibility of the survival of the fungi growing saprophytically in solutions in heavily-manured soils.

In *Ustilago* the basidium or promycelium which arises from the resting chlamydospore resembles in appearance a stout germ tube. When young it contains a single fusion nucleus (Fig. 150a). When mature it is (usually but not always) divided by transverse septa into four cells, each of which contains a haploid nucleus. These nuclei are produced by two divisions of the fusion nucleus (Fig. 150b, c, d). Each of the four nuclei divides again and one of the products of each division passes into one of the four lateral basidiospores or sporidia formed by the basidium (Fig. 150e). There are, therefore, four nuclei left in the basidium. These

Basidiomycetae—Heterobasidiomycetes

may divide again. In this way nuclei can be provided for several crops of spores and thus the number of spores cut off is irregular. The heterokaryotic phase may be started by the fusion of cells of haploid mycelia arising from the germ tubes of two spores, by the fusion of two germ tubes soon after germination, by the fusion of two spores or even by the transfer of nuclei between adjacent cells within the basidium itself. In this last case the transfer is accomplished by the development of buckle-like processes comparable with clamp connexions.

At one time it was believed that the Basidiomycetae were derived from the Phycomycetae direct; and that the phycomycte conidiophore had given rise to the basidium. When this was accepted as true, the Ustilaginales were regarded as the linking forms between the two classes and were distinguished from the true Basidiomycetaceae as the Hemibasidiomycetes by reason of their less definite type of basidium cutting off an irregular number of spores. It seems better to regard the septa in the basidium of the smuts, as in other orders, as a derived character and to take the same view of the diversity of spore numbers and of the processes by which the heterokaryophase is initiated.

Ustilaginaceae—Within the genus *Ustilago* there are species which form their resting spores within tissues of very varying types. These spores are formed within the developing ovaries only in the case of most of the smuts attacking cereals. They are formed in the anthers of the flowers of *Lychnis dioica* by *Ustilago violacea* (Pers.) Fuckel. In *Ustilago longissima* (Sow. ex Schlecht.) Meyer the spores replace the leaf tissues of certain grasses. Exceptionally, as in *Ustilago maydis* (DC.) Corda, Maize Smut, they may be formed within all organs including the roots. In most species attacking cereals, typified by *U. avenae* (Pers.) Rostr., Loose Smut of oats, the fungus is present as resting mycelium or ungerminated spores on the outside of the grain when it is sown. Seedlings soon become infected. They are fairly normal in appearance, though there may be some stunting and loss of colour. Host tissues are not killed, except for those of

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the developing ovary, which are broken down and replaced by chlamydospores. These spores are more or less spherical, minutely echinulate, 4-8 μ in diameter. They are set free by the breakdown of the external tissues. They are carried to, and remain dormant on the outside of, healthy grains. The germination of the chlamydospores coincides with the germination of the oat grain. Basidiospores are produced; they measure 2-7 \times 4-7 μ . A heterokaryotic mycelium is established by fusions occurring between cells of the basidium or between abstricted basidiospores. Penetration is secured about the base of the plumule and must take place before that organ is an inch long, otherwise the tissues are able to resist the attack.

This type of smut can be controlled by killing the spores on the outside of the grain by treatment, before sowing, with formalin solution or dust. Copper carbonate dust is used for those varieties of host which are sensitive to formalin.

Some species, such as *U. nuda* (Jens.) Rostr., Loose Smut of wheat and barley, cause infection of new host plants at flowering. The spores formed in the ovaries of the plants originally infected are set free at that time due to the breakdown of the external tissues. Penetration by the hyphae is secured at once and the grain sown the following season already contains the mycelium which has invaded all parts of the embryo except the roots and young leaf primordia.

Control of the disease is secured by a treatment the essential feature of which is soaking the grain, before sowing, in water at 54° C. This temperature kills the internal mycelium without damaging the embryo.

BASIDIOMYCETAE—RELATIONSHIPS

THE WRITER's views on the evolution of the Basidiomycetae and the order in which the various groups have evolved within that class has been indicated in the preceding pages. Before the salient points are emphasized again it is as well to give an account of one at least of the many differing views still current.

Wilson (1950) following de Bary's views suggested that the Uredinales were derived, before the evolution of the Angiospermae, from an ascomycetous fungus which formed spermatogonia and perithecia on a gymnospermous host. In this fungus the cells of the ascogenous hyphae failed to produce asci (as the result of a mutation); but separated, forming chains of binucleate spores: thus the perithecium became transformed into an aecidium. The aecidiospores were unable, as in present day rusts, to reinfect the host on which they were formed. They were numerous and, by chance, some alighted on a new compatible moss or fern host. The binucleate mycelium developed on this new host gave rise to repeating spores, uredospores, and ultimately to spores in which the conjugate nuclei fused, teleutospores. These on germination gave the rust type of basidium, bearing uninucleate basidiospores which reinfected the original gymnosperm host. Thus the complete life cycle of a heteroecious rust is supposed to have evolved. From the heterokaryotic mycelium on the fern, it is thought that new forms were evolved including both parasites on ferns resembling forms now placed in the Auriculariales and, by adoption of the saprophytic habit, forms leading to those included in the Homobasidiomycetes in the present classification. This is a most interesting line of reasoning; but the writer feels that the facts marshalled in the next paragraph are of such fundamental importance as to support the

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scheme of classification given for the Basidiomycetae in earlier pages.

It is generally accepted that the septate hyphae of the Ascomycetae and Basidiomycetae are more highly evolved than the coenocytic mycelia of the Phycomycetae. It is logical, therefore, to apply the same argument to the sporangium or basidium which is septate in the Heterobasidiomycetes but not in the Homobasidiomycetes or in the Ascomycetae, where it is represented by the ascus. The majority of Homobasidiomycetes are known to have well developed clamp connexions, which link with the crosier structures occurring in the Ascomycetae. Clamp connexions are either entirely absent from the rusts and smuts or only poorly and casually developed. To evolve the Homobasidiomycetae from the Heterobasidiomycetae would involve believing that this very characteristic type of structure had been developed independently in the Ascomycetae and again in the Basidiomycetae. The suggestion that a large-scale evolution of saprophytic from parasitic forms has taken place is contrary to the generally accepted view that parasites throughout the plant kingdom are derived forms. The highly specialized nature of their life histories marks them as forms specially adapted to restricted habitats. The appearance of the resistant probasidium enables these total parasites to survive the death of their host plant. Parasitic forms in the Homobasidiomycetes react to this problem by reassuming a saprophytic mode of life. Their parasitism is not obligate and is usually much less restricted in its host range.

DEUTEROMYCETAE (FUNGI IMPERFECTI)

IN THESE imperfect forms the mycelium is septate. They often reproduce by conidia. Some few produce no reproductive spores at all. No asci or basidia have been found. It is thought that in most the power to produce a perfect stage has been lost. In a few, it is more probable that the connexion between the imperfect fungus and its perfect stage has not been established experimentally. Whenever the connexion between one of these conidial stages and a perfect stage is proved, the imperfect fungus can be reclassified within the appropriate perfect group. Examples of this have been referred to repeatedly throughout the preceding pages—Graphium with Ophiostoma, Aspergillus with Eurotium. Smith (1938) states that 1,200 genera and 24,000 species are referable to the class. The British species have been dealt with in detail by Grove (1935, 1937).

The Deuteromycetae are usually minute fungi. There are in the group many parasites responsible for serious plant and animal diseases. The species are divided into three orders. These are distinguished from each other by the manner in which the conidia are borne, in the way outlined below. A fourth division is usually employed to house those forms whose reproductive spores are unknown. This group is called Mycelia Sterilia.

Spores borne within a cavity

Sphaeropsidales—In this order pycnidia are formed. That is to say a flask-shaped sporophore is produced in which the hymenium bearing the spores lines a cavity opening to

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the outside by a neck or ostiole. The hymenium is surrounded by one or more layers of hyphae forming a peridium (Fig. 151).

Melanconiales—Here the spores are borne in aecervuli. They arise on massed conidiophores growing from a stromatic base in a cavity of which the outer wall is formed

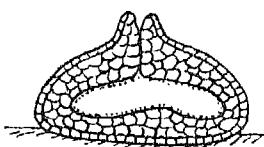


Fig. 151. *Phoma acuta*.
Pycnidium (after Dennis,
1946)

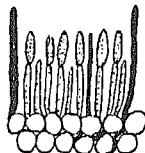


Fig. 152. *Colletotrichum
atramentarium*. Aecer-
vulus

not by fungus tissue but by the tissues of the host. The pustules break through the host epidermis or bark and lie freely exposed (Fig. 152).

Spores borne outside the matrix

Hymomycetales—These species have superficial conidiophores which may be free from each other or united into structures of varying shape (Fig. 153).

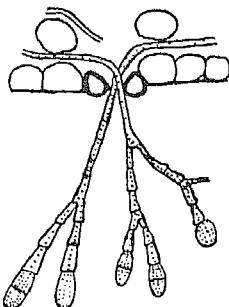


Fig. 153. *Cladosporium fulvum*.
Spore-bearing hyphae emerging
from the matrix

Subdivisions within each of the three orders depend on the shape of the spores and the number of cells of which they are composed. Further, within each subdivision, the

Deuteromycetae (Fungi Imperfecti)

classification separates species having colourless and coloured spores. In the Sphaeropsidales, for example, there are four groups as follows.

Spores one-celled	
(a) colourless	.. Hyalosporae
(b) coloured	.. Phaeosporae
Spores two-celled	
(a) colourless	.. Hyalodidyme
(b) coloured	.. Phaeodidyme

The third and fourth groups contain respectively fungi in which the spores have two or more septa or are elongated and worm-like.

In addition to those examples already discussed in connexion with their perfect stages, one species from each order will be described to serve as examples for the whole class.

SPHAEROPSIDALES

The genus *Phoma* belongs to this order. Grove (1935) lists over 150 British species of *Phoma*. They are distinguished from each other mainly by the host plants on which they occur. Dennis (1946) has emphasized the danger of according specific rank to forms of *Phoma*, when the decision to do so is based on this criterion only. He has shown by culture work that the same fungus may be found under a number of different names in the existing classifications of the genus

Fig. 154. *Phoma acuta*. Group of ostiolate pycnidia on dead stem of *Urtica dioica* (after Grove, 1935)



and, perhaps more surprisingly, that several different fungi may still be found grouped under the one name.

Phoma acuta Fckl. is one of three distinct species isolated by Dennis (1946) from dead stems of *Urtica dioica* in south-east Scotland. Grove (1935) found it to be rather common in Britain generally. It is fairly readily recognized in nature because its pycnidia are much larger than those of the other species of *Phoma* occurring on this host (Fig. 154).

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The pycnidia are up to 500 μ in diameter. They are formed in groups based on the wood of the nettle stems. They are conical to globose in shape, black in colour, shining and have a well-marked apical papilla by which the pore of the conical ostiole opens to the outside. At first they are completely covered by the epidermis. Later the papilla breaks out through this layer. Finally, when the soft outer tissues peel away, the groups of pycnidia are fully exposed (Figs. 151, 154). The oblong spores are expressed through the ostiole as a faintly cream-coloured exudate. They are biguttulate and average $4.7 \times 1.8 \mu$.

MELANCONIALES

Colletotrichum atramentarium (Berk. and Br.) Taubenh., a fungus which belongs to the Melanconiales, causes Black Dot disease of potatoes. In Britain it is commoner as a saprophyte, forming its black sclerotia on the dead stems and tubers of the potato. It seldom causes disease of any importance in this country. It is much more troublesome in warmer and drier climates. The cortical tissues are attacked particularly near the base of the stem. Both sclerotia and spore-bearing pustules appear on the attacked parts.

The sclerotia may be minute or measure up to 0.5 mm. in diameter. They frequently bear a large number of dark-brown stiff bristles or setae varying in length up to 350 μ , which are characteristic of the genus. The accervulus also carries the typical setae. The spores are oblong, pinkish in the mass and measure from $17-22 \times 3-8 \mu$ (Fig. 152).

The fungus survives the winter on decaying parts of the potato plant, probably in the form of sclerotia. If all potato waste material is burned this will minimize soil infection. Care should be taken also not to plant tubers which bear sclerotia on their skins.

HYPHOMYCETALES

Cladosporium fulvum Cke. belongs to this order. It is the organism which causes Leaf Mould of tomatoes. This is the most serious fungus disease of tomatoes growing under glass

Mycorrhiza

in Britain. Outbreaks occur most commonly in June or July starting on the lower leaves of the plants. The fungus causes pale yellow spots on the upper surfaces of the attacked leaves. If the under-surface of the latter is examined, patches of mould may be seen. These are grey in colour at first but darken to a purple-brown as they get older. At this last stage the spores are being produced. Sections through attacked leaves show the conidiophores emerging through the stomata, principally on the under-surface of the leaf. They are septate and have a jointed appearance. They are olivaceous in colour. Hyaline or faintly brown conidia are borne at the ends of the conidiophores or subterminally (Fig. 153). Mature conidia are usually uniseptate, uninucleate and measure $10-20 \times 4-6 \mu$.

Mycelial growth and spore production are favoured by a damp atmosphere and a good deal can be done to prevent the disease from becoming epidemic by improving ventilation. Some commercial varieties show considerable resistance to Leaf Mould. Spraying with a colloidal copper compound in conjunction with an oil emulsion gives protection to susceptible varieties. Thorough cleaning of the tomato houses after the plants are removed at the end of the growing season is to be recommended. This prevents the fungus surviving on fragments of decayed tomato plants and bringing about infection during the next growing season.

MYCORRHIZA

THE TERM mycorrhiza means literally fungus root. The symbiotic relationship between fungi and the roots of plants, which is described by this name, occurs in the Angiospermae, the Gymnospermae and the Pteridophyta. If the

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definition is widened to include any case in which fungi live apparently symbiotically within other plants then members of the Bryophyta—both Musci and Hepaticae—also show the relationship. It should be remembered that there are many species in all the plant groups in which there appears to be no mycorrhizal relationship. A symbiotic relationship between various fungi and members of the only other plant group not involved in mycorrhiza formation—the algae—results in the formation of lichens. These composite organisms are described in the next chapter.

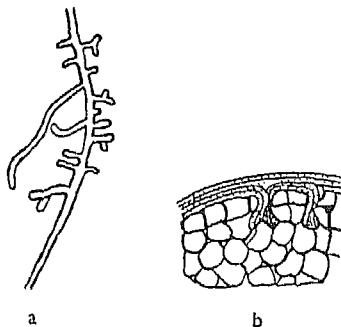


Fig. 155. Scots Pine. a Coraloid roots with ectotrophic mycorrhiza; b transverse section of outer part of root showing external layer of hyphae and hyphal masses penetrating the cortex

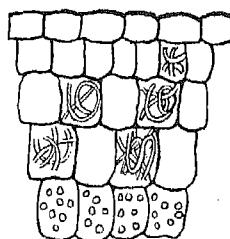


Fig. 156. Bird's Nest Orchid. Transverse section of outer part of root showing endotrophic mycelium in the cortical cells; the infected region is free from starch

The best known mycorrhizae are those which occur associated with coniferous and broad-leaved forest trees, with heaths and with orchids (Rayner, 1927; Rayner and Neilson-Jones, 1944).

There are two main types of mycorrhiza, ectotrophic and endotrophic. In neither type of relationship is the morphology of the subaerial parts of the plant altered visibly; but the underground parts may be markedly changed in appearance, especially in the case of ectotrophic mycorrhiza. Ectotrophic mycorrhiza occurs in such common trees as oak, lime, birch, beech, poplar, Scots pine and larch. The mycorrhiza is endotrophic in members of the Ericaceae and

Mycorrhiza

Orchidaceae, in the maple, the horse-chestnut and, as has been recently shown, in the She oak, *Casuarina equisetifolia* Forst. (Bose, 1947) and in the Cistaceae (Boursnell, 1950).

In the ectotrophic mycorrhiza of a tree such as the Scots pine many of the lateral roots assume a swollen and stunted appearance so that they are coraloid in form (Fig. 155a). These laterals are enveloped in a mass of fungal hyphae which performs the absorptive function normally restricted to root hairs. Some of the hyphae pass in between the cells of the outer layers of the root and can be seen in cross sections of that organ filling the intercellular spaces of the cortex, thus surrounding its constituent cells (Fig. 155b). These hyphae are said to form the Hartig-net.

In the endotrophic mycorrhiza of the saprophytic "Bird's Nest Orchid", *Neottia nidus-avis*, the hyphae of the fungus are within the root and inside the cells of the outer cortex (Fig. 156). In a transverse section of the root it is usually possible to see various stages in the digestion of these intracellular hyphae.

The distinction between ectotrophic and endotrophic mycelia is not absolute. Intermediate types occur. Nor yet in endotrophic mycorrhiza are the fungal hyphae always confined to the root. In the most extreme cases, such as the heaths, the endophyte sends its fine hyphae throughout the plant. All organs are infected in *Calluna vulgaris*, even the capsular fruits. As a result, seeds carry the hyphae and seedlings become naturally infected at the time of germination. The same type of relationship as exists in *Calluna* occurs also in *Casuarina equisetifolia*.

The seeds of both Orchidaceae and Ericaceae are minute with but scanty food reserves. In both families it has been shown that satisfactory germination of the seeds will not take place in the absence of the mycorrhizal fungus. By growing seedlings of plants belonging to various families in pure culture, it has been proved further that, even when germination does take place, satisfactory subsequent growth is obtained only if the mycorrhizal fungus is added to the culture. Thus it appears that, in some cases, the mycorrhizal

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relationship is obligatory on, and, in others, at least very desirable for the non-fungus partner. It would appear probable that an obligate relationship exists in the case of all saprophytic plants.

The benefits of the mycorrhizal relationship to the non-fungus partner are certainly two-fold and possibly three-fold. There is an increased absorbing surface and higher efficiency of absorption with mycorrhiza roots as opposed to normal plant roots absorbing by root hairs. This means that plants with mycorrhiza can compete successfully against those without mycorrhiza for soil nutrients which are in short supply. The difference is very marked among seedling trees growing on poor soils. The germination of the seeds of certain mycorrhiza-forming orchids takes place in the absence of the fungus, if the medium on which the seeds are planted supplies sugar. This indicates that carbohydrate supply is one of the functions of the fungus. The destruction of the hyphae of the endophyte as in *Neottia* must yield both carbohydrate-containing and nitrogen-containing products of value to the metabolism of the other partner. It has been claimed, too, that there is fixation of atmospheric nitrogen by the endophyte in the heaths.

The benefits received by the fungus symbiont are more difficult to understand. The internal hyphae receive protection and it has been suggested that growth-promoting substances may be passed to them. The cells of the root cortex in *Neottia*, which contain the hyphae, are the only ones from which starch grains are always absent. Presumably, therefore, the carbohydrate has passed to the endophytic mycelium which derives benefit during the pre-digestion stage.

The fungi associated with ectotrophic mycorrhiza belong chiefly to the Hymenomycetales and include species of *Boletus*, *Amanita* and *Lactarius*; but members of the Gasteromycetales such as *Scleroderma* and, among the Ascomycetae, the Truffle fungi, belonging to the order Tuberales, are also involved. Among the endophytic fungi most of those found in orchids are sterile stages of species of *Corticium* which are

Mycorrhiza

placed in the imperfect genus *Rhizoctonia*. But the endophytic fungus in *Gastrodia elata*, a saprophytic orchid occurring in Japan, is *Armillaria mellea*. Those tubers which contain the mycelium produce flowers, those without it do not. The outer layers of the tuber contain thick-walled hyphae. Those layers further in contain hyphae which are thinner walled. The hyphae within the tuber are connected with the rhizomorphs of the fungus in the soil and these may be simultaneously parasitizing the roots of adjacent oak trees. The endophyte of *Calluna vulgaris* is the deuteromycete *Phoma radicis* var. *callunae*, that of *Casuarina equisetifolia* is *Phomopsis casuarinae* F. Tassi. The fungi inhabiting saprophytic liverworts and a good many herbaceous seed plants belong to the Phycomycetae. Among the latter, the relationship seems to be much more casual. One such endophyte has been shown to be a zygomycetous fungus belonging to the genus *Rhizophagus* of the family Endogonaceae.

The fungus flora associated with particular kinds of trees is often characteristic. Thus, *Amanita muscaria* Fr., the Fly Agaric, and *Boletus scaber* Krombh. are two species occurring under birch, while *Boletus elegans* Fr. is similarly associated with larch.

In some cases it has been proved that the mycorrhizal relationship of a particular species of green plant need not always involve the same species of fungus. *Pinus sylvestris* has been shown to form mycorrhiza with fourteen different species belonging to the Hymenomycetales and Gasteromycetales. It has also been shown that the same root may be simultaneously occupied by two mycorrhiza fungi belonging to different classes and exhibiting entirely different mycelial characters.

In species of *Lolium* two unidentified endophytic fungi have been described which occur in all the parts of the plant above ground. They may even pass to the next generation via the grain. Yet neither is the presence of these fungi necessary for the normal growth of the plants nor does it cause any damage to the grass.

The nature of the mycorrhizal relationship has been

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variously interpreted. It is best to regard it as a genuinely symbiotic one. It has been suggested that the relationship has evolved from one in which the fungus was originally parasitic. The fact that the mycorrhiza fungus in the orchids does sometimes get out of the control of the higher plant and cause damage, and the fact that *Armillaria mellea* is normally an active parasite have been cited in support of this view. It seems to the writer more probable that the habit has originated as a result of the proximity of non-fungus plants to the hyphae of the numerous fungi which grow as saprophytes in the organic litter on the earth's surface. That is to say that the relationship is derived from a previously saprophytic one and indicates how parasitism may have arisen rather than that it has been derived from a previously parasitic condition.

LICHENES

THESE are compound organisms composed of an alga and a fungus living in an intimate symbiotic relationship (Lorrain Smith, 1921). The thallus is made up of colourless fungal hyphae interspersed with green algal cells. The algal part consists of rounded portions (gonidia) derived from recognizable species of free-living blue-green or green algae. It may be grown in culture independent of the fungus partner. The fungus, on the other hand, though it is related to some free-living species, is not identical with any. It cannot be grown apart from its algal partner for any length of time. Thus it has undergone some fundamental modification. The fungi which form part of lichens are all referable to the Ascomycetace with the exception of three tropical genera. In these the fungus is some member of the

Lichenes

Basidiomycetae. They need not be specifically referred to further here.

In the more primitive lichens the shape of the thallus corresponds with that of the alga. This is true of forms with a gelatinous thallus such as *Collema pulposum* Ach. which occurs in limestone districts. In the majority of cases the lichen has a characteristic form of its own due to the predominating fungus partner, as in species of *Cladonia*.

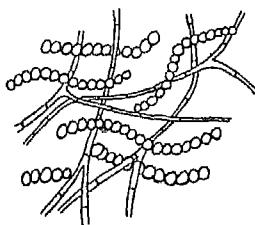


Fig. 157. *Collema pulposum*. Part of homoiomerous thallus teased out

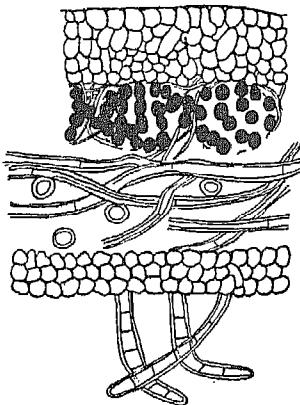


Fig. 158. *Peltigera canina*. T.S. heteromerous thallus showing fungal pseudoparenchyma, algal layer and anchoring rhizoid hyphae

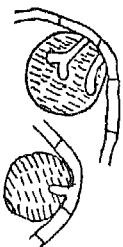
Blue-green algae which occur in lichens include *Chroococcus*, *Gloeocapsa* and filamentous forms such as *Scytonema*, *Nostoc* and *Rivularia*. The green alga *Protococcus* and similar forms are present in the greater number of the larger lichens and the filamentous genera *Trentepohlia* and *Cladophora* are also represented. These algae only reproduce themselves vegetatively and usually by simple division.

The algal cells may be scattered throughout the thallus. In this case the lichen is described as homoiomerous (Fig. 157). *Collema* is an example of this condition. Frequently the algal cells are arranged in a definite layer near the upper surface of the thallus. This is the heteromerous type

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of organization. It occurs in *Peltigera*, *Physcia*, *Sticta*. It is possible to distinguish in the heteromeric lichens an upper cortical region, the layer containing the algal cells or filaments, a loose medullary region and, finally, a lower cortex (Fig. 158).

The fungus threads may be normal in appearance and thin-walled or they may have thick walls which give them a structural value as well as enabling them to protect the thallus against desiccation. There is a marked tendency to the formation of pseudo-parenchyma. Some hyphae are



[Fig. 159. *Physcia*.
Hyphae investing
and penetrating
algal gonidia

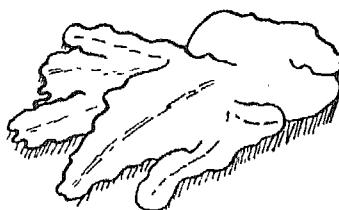


Fig. 160. *Peltigera canina*.
Portion of leafy (lobed)
thallus

united together to form rhizoids which have both an anchoring and an absorbing function (Fig. 158). Those hyphae which grow in the region occupied by the algal gonidia invest the algal cells closely and may penetrate them, forming haustoria (Fig. 159).

The fungus produces a perfect stage similar to that of a free-living Ascomycete.

There are three main types of thallus development in the lichens, though the form of the thallus may occasionally change from one type to another during the life of an individual lichen. First, there are the crustaceous or crustose types which form a crust of varying thickness over the substratum of tree trunk, rock or soil. In this group may be placed the gelatinous thalli of *Collema* and the thin, dry thallus of *Verrucaria maura* Wahlenb. growing on the

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seemingly bare rocks of the sea shore near high water mark. The second type are the foliose or leafy lichens. These are spreading and one-lobed to many-lobed. They are typified by *Peltigera* (Fig. 160) and *Parmelia*. Third are the fruticose or shrubby lichens. These arise from a basal point. The thallus may vary from short stiff lobes as in *Ramalina* (Fig. 161), to long pendulous strands as in *Usnea*. In *Cladonia* there is a basal crustose or lobed thallus and an upright, simple or branched stalk, which may open out into a cup.

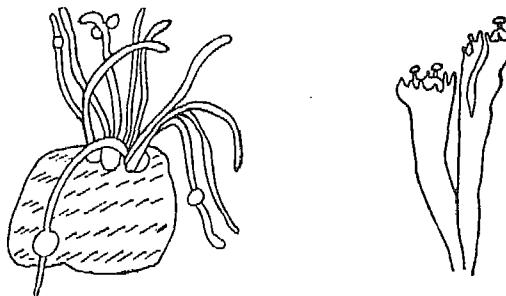


Fig. 161. *Ramalina*.
Shrubby type of thallus

Fig. 162. *Cladonia*. Upright,
cupped portion of thallus,
bearing apothecia round its
edge

The reproductive structures are borne on the tips of the stalks or round the edges of the cups (Fig. 162).

There is a number of specialized vegetative structures peculiar to the lichens. Of these the most important are the sorocidia. These consist of one or a number of algal cells closely surrounded by hyphae. They occur collected in grey pustules on the thallus surface from which they are readily detached. They thus give an excellent means of reproduction, for a new thallus may develop from each of them. They may be seen forming a powder on bare ground or tree trunks representing the first stage in the growth of lichen thalli. Their importance is enhanced by the fact that reproduction of the lichen by the fungus spores is uncertain, as the fungus will not long survive in the absence of gonidia.

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The fungus reproduces by apothecia (Fig. 163) or perithecia of similar structure to those produced by free-living members of the Ascomycetae. The classification of the lichens is based on the characters of these fructifications. The apothecia in the lichens have a much higher proportion of sterile paraphyses to asci than in the Ascomycetae. They may consist entirely of fungal hyphae as in *Rhizocarpon*, belonging to the Lecideaceae, or, in more highly developed types such as *Lecanora*, belonging to the Lecanoraceae,

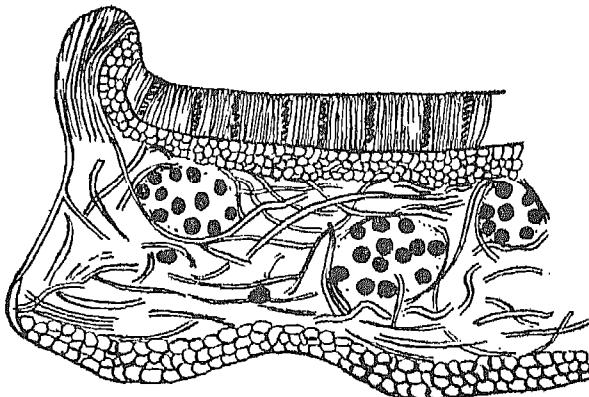


Fig. 163. *Physcia*. Section through portion of thallus bearing apothecial hymenium on its upper surface

there may be an outer, protecting margin consisting of gonidia and hyphae. Apothecia vary in size from about 0.25 mm. to over 10 mm. in diameter. Lichen perithecia are usually small bodies more or less immersed in the thallus. Each may be surrounded by a wall, or the wall may be reduced or absent round the sunken, basal part of the perithecium. In some genera such as *Endocarpon* in the Dermatocarpaceae, gonidia occur in the perithecium along with the asci and escape through the ostiole along with the ascospores. New thalli may develop in this way.

It is possible to trace the same series of reductions in the sexual organs of ascolichens as it is in normal ascomycete fungi. In *Collema pulposum* Ach. both organs are present and

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the process is complete. There is a coiled ascogonium with a multicellular trichogyne. Numerous non-motile antheridia or spermatia are contained in a flask-shaped spermogonium. These are released to be washed about on the surface of the thallus until they ultimately reach and fuse with the trichogyne. After this fusion the ascogonium gives rise to ascogenous hyphae some of which produce asci and others paraphyses. The latter are more numerous than in ordinary Ascomycetaceae. In *Peltigera canina* Willd., on the other hand, red apothecia are produced at the edges of the lobed thallus; but there is no trace of either type of sexual organ.

The algal partner carries on photosynthesis and supplies carbohydrate food, while the fungus threads can absorb water, from rain or sometimes from the soil, and salts which they pass to the alga with, possibly, peptone in addition. The two plants composing the thallus both derive benefit. The fungus is incapable of living without the alga. Thus the condition of affairs approaches that which is found in the relationship between the obligate parasite rust fungi and their higher plant hosts. The relationship is often regarded as an example of benevolent parasitism on the part of the lichenized fungus, towards its algal host. Yet each lichen is a biological unit. Some of the organic products of their metabolism are found only in lichens. This is true of the lichen acids which are abundantly produced.

Lichens reach their most luxuriant development in a moist atmosphere under abundant light; but their structure is adapted to life under difficult conditions. They are able to withstand extremes of drought and nearly always live under xerophytic conditions. They are the first plant pioneers on barren rocks and soil. They form a very important part of the vegetation of great tracts of arctic and mountain regions. They inhabit acid moorlands, the bark of trees, sandy places and sea shores.

Verrucaria maura Wahlenb. is a common, black, crustose lichen occurring in the spray zone on rocky shores. It is submerged by spring tides (Dunn, 1941). *Xanthoria parietina* Th. Fr. forms bright yellow patches on sunny roofs, rocks,

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etc. *Usnea barbata* Web. is a common, pendulous, tree-inhabiting form which, in Britain, may attain lengths of 35 cm. or more. *Cladonia rangiferina* Web. is Reindeer Moss and forms a large part of the pasture of these animals in the arctic. *Rhizocarpon geographicum* (L.) DC. has almost a world wide distribution in mountainous parts.

Apart from their natural importance, referred to above, lichens yield products which are sources of a number of beautiful dyes. Probably the best known is orchil or litmus, which is obtained particularly from *Roccella tinctoria* DC. *Cetraria islandica* Ach., Iceland Moss, is still sometimes prepared for human food in northern countries.

The lichens are polyphyletic with regard to both their symbionts. Their detailed classification is rendered difficult as, usually, the characters of both symbionts are considered in determining genera and species. However, the ascolichens fall into two main groups: (1) the Gymnocarpeae in which the fructifications are more or less saucer-shaped or disc-shaped. They are of the discomycete (*Peziza*) type. (2) The Pyrenocarpeae with perithecial fructifications, comparable to those of the Pyrenomycetes among free-living Ascomycetaceae.

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