DISPERSAL IN FUNGI

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BY

C. T. INGOLD

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PREFACE

THIS little book is intended to give a picture of dispersal in fungi that may be of interest to all those concerned with fungi as living organisms. Another writing a book of this title would, of course, have produced a very different one. A plant pathologist might have been concerned largely with the spread of plant pathogens and with the origin and development of epiphytotics. A taxonomist might have emphasized the snares which parallel evolution, in connexion with dispersal, lays for the searcher after a natural classification. That new-comer to the scientific arena, the aerobiologist, would have made the subject of spores in the air the major part of the book. I also have not attempted a neatly balanced work, but have given emphasis, though not, I hope, undue emphasis, to those aspects of the subject that have interested me most.

The present essay is not an exhaustive treatment, for such would have necessitated a very much bigger book crammed with references. It will, indeed, be clear that the references cited form by no means a complete bibliography of spore dispersal.

For ease of reading, authorities following the specific names have been omitted from the text, but an appendix gives a list of all fungal species mentioned, with the authorities cited.

Most of the figures in this book are my own, but some are from other sources. In this connexion I have to thank the following: the Director of the Royal Botanic Gardens, Kew, for permission to base Fig. 67 on a beautiful half-tone picture illustrating an unpublished chapter of Buller's *Researches* deposited at the Herbarium, Kew; Messrs.

Longmans, Green & Co. for permission to base certain pictures (Figs. 3, 12, 13, 46, 47, and 48) on drawings published in the first six volumes of Buller's *Researches on Fungi*; the University of Toronto Press and the Royal Society of Canada for permission to copy part of a figure from Buller's *Researches on Fungi*, vol. vii, as my Fig. 62; and to the editors of *The New Phytologist*, *The Transactions of the British Mycological Society*, and *Farlowia* for allowing me to use a number of figures that have appeared in those journals.

My thanks are also due to E. K. Horwood, who took the photographs reproduced as Plate I and Plate II A, and to C. E. B. Dobb, who was likewise responsible for Plates IV and VI. Plate VIII, illustrating the Ulster method of testing for seed-borne pathogens, is reproduced by kind permission of Professor A. E. Muskett and Dr. J. Colhoun from their book *The Diseases of the Flax Plant*.

C. T. I.

BIRKBECK COLLEGE
December 1952

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INTRODUCTION

DISPERSAL is one of the fundamental problems that has faced the Fungi* and much of their beauty of structure is associated with the solution of this problem. In fungi the vegetative part is usually hidden away as a feeding mycelium in the nutrient substratum and the conspicuous part is an apparatus concerned with the production and liberation of spores.

A spore to students of archegoniate plants (Bryophyta and Pteridophyta) is definable as a unicellular asexual reproductive body formed within a sporangium following meiosis. However, the mycologist uses the term in a much wider sense. To him a spore is any simple reproductive unit, often unicellular but frequently multicellular, and usually with some food reserve. He recognizes many different kinds of spore: zoospores, sporangiospores, chlamydospores, zygospores, oospores, ascospores, uredospores, basidiospores, teleutospores, brand spores, and various types of conidia such as pycnidiospores, aleuriospores, phialospores, arthrospores, and blastospores. With the possible exception of ascospores and basidiospores none of these can be considered as homologous with the spores of archegoniate plants. However, all these kinds of spore agree in being microscopic, normally devoid of vacuoles and, more often than not, unicellular.

Not all spores are units of dispersal, some are merely resting-spores that tide over an unfavourable season, usually winter. This is true of most zygospores and oospores and of the teleutospores of rusts. However, certain spores,

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* The term 'Fungi' is used here in its more restricted sense as synonymous with 'Eumycetes' and excludes bacteria, Actinomycetes, and slime moulds.

such as the brand spores of some smuts (e.g. *Ustilago avenae*, the loose smut of oat), are concerned both with hibernation and with dispersal.

The size and shape of fungal spores vary considerably. Many species have very small spores of only 1–2 μ in diameter. At the other extreme are the oval ascospores of certain lichens: *Pertusaria velata* with a unicellular spore up to 310×100 μ and *Varicellaria microsticta* with an even larger two-celled spore (up to 350×115 μ). Spores of this size are just visible to the naked eye and are of much the same size as the smallest seeds of flowering plants (Fig. 1). It is interesting to note that those phanergams, mostly orchids and saprophytes, which produce very small seeds would seem to be reversing the course of evolution. Their seeds have become so simplified that they are almost spores and, correlated with the decrease in size and differentiation, the number produced has greatly increased.

In spite of the great variation in the size and shape of fungal spores, the vast majority are unicellular, spherical, or ovoid, with a diameter falling within the size limits 5 μ to 50 μ.

Except for the naked zoospores of water moulds, spores have cell-walls usually quite thin, but becoming very thick in some species, especially in those forming subterranean fruit-bodies (e.g. *Elaphomyces granulatus*). The spore-wall is mostly transparent and colourless, but in a number of fungi it is coloured and quite frequently black. Sometimes the colour of a spore is not entirely due to the pigment in the wall. Thus the red uredospores of *Puccinia graminis* owe their colour to a combination of a brown wall colour with an orange pigment in the cytoplasm, although in this species mutant strains are known* where one or the other pigment is suppressed, giving in one variety greyish-brown

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* Newton, Johnson, and Brown (1930).

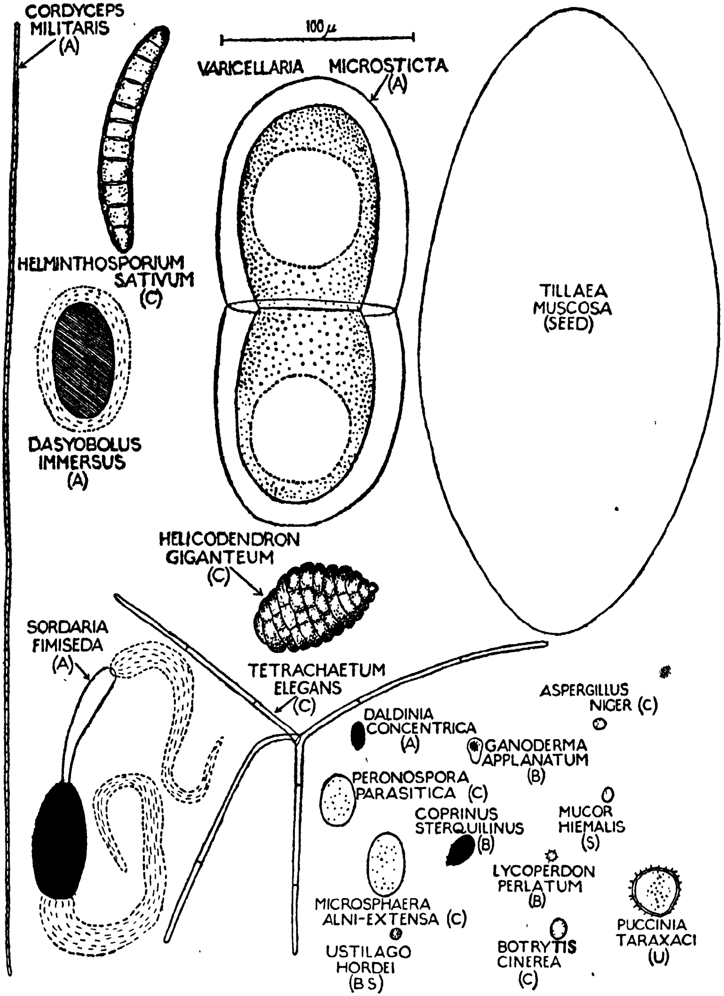

FIG. 1. Size of spores. Outline of minute seed of *Tillaea muscosa*, seven exceptionally large fungal spores, and eleven spores of more usual size and form. All drawn to same scale. Type of spore indicated in brackets with each species.

A, ascospore; *B*, basidiospore; *B.S.* brand spore; *C*, conidium; *U*, uredospore; *S*, sporangiospore.

uredospores and in the other orange ones. In most fungi the spore-wall is smooth, but it may be wrinkled, pitted, warted, spiny, or alveolate.

An outstanding feature of most species is the enormous spore production. Students of green plants and of animals are very familiar with the principle of the necessary wastage of reproductive units, but in Fungi this wastage seems to reach its extreme expression. On the average not more than one or two spores from each individual fungus succeed in their reproductive function, since each species is more or less in equilibrium with its environment and its numbers, though they may fluctuate from year to year, show no steady increase.

Many estimates of spore output have been made, but here only a few examples are selected to give a clear picture of the gigantic scale of spore production in a wide range of types. A big specimen of the giant puff-ball (*Calvatia gigantea*) has been estimated to contain 7,000,000,000,000 spores.* The large bracket fungus *Ganoderma applanatum* may liberate 30,000,000,000 spores a day, apparently maintaining this output for the whole six months (May to October) of its spore-fall period.† The small apothecium of the cup-fungus *Sclerotinia sclerotiorum* has been shown to produce 30,000,000 ascospores.‡ A perithecial stroma of the flask-fungus *Daldinia concentrica* may discharge over 100,000,000 spores each day.§ In the stinking smut of wheat due to *Tilletia caries* a single diseased grain may contain over 12,000,000 brand spores.|| A colony of blue mould (*Penicillium* sp.) 2·5 cm. in diameter may bear 400,000,000 conidia.

However, production of spores is not always on this gigantic scale and, especially in aquatic fungi, spore output

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* Buller (1909). † White (1919). ‡ Stevens (1911).

§ Ingold (1946). || Stakman and Christensen (1946).

may be quite low. For example, in the Chytridiales the zoospores formed by each individual fungus are often less than 100. In *Rhizophydium planktonicum* (Fig. 2), a parasite of the diatom *Asterionella* so abundant in freshwater plankton,* the number of spores liberated from the single sporangium which each individual forms is only ten to twenty, yet this fungus manages to survive and is probably very common in lakes and reservoirs. In some land fungi the spore output is also quite small. Thus in the coprophilous species *Dasyobolus immersus* and *Sordaria fimiseda* the total spore production from each fruit-body is not great. Here

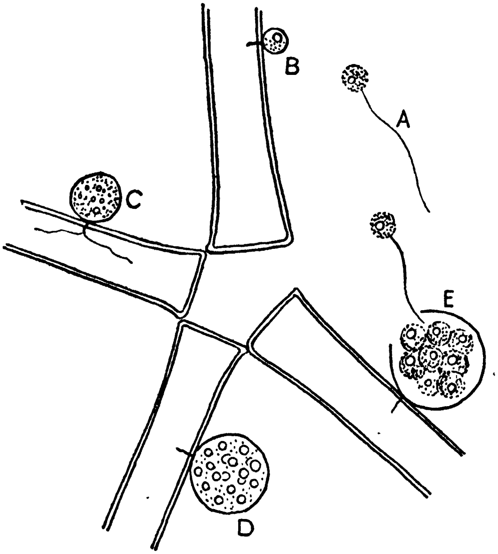

FIG. 2. *Rhizophydium planktonicum* parasitizing the diatom *Asterionella*. × 1,000.

A, zoospore; *B*, young thallus; *C*, older thallus; *D*, thallus with rhizoids and single sporangium; *E*, zoospores escaping from sporangium.

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* Canter and Lund (1948).

the relatively small numbers may be correlated with the great efficiency of the spore dispersal arrangements and with the large size of the spores. As with many seed plants, so with the fungi there seems to have been a struggle between two tendencies: the tendency to produce an enormous number of very small units readily dispersed but each with a relatively small food reserve and thus with a relatively poor chance of success, and the tendency to concentrate on a smaller number of larger units not, perhaps, so readily dispersed but with a greater chance of succeeding.

An important attribute of a spore from the point of view of dispersal is its viability, and spores vary greatly in this respect. The fact that a spore may be transported a long distance is of no significance if at the end of its journey it is incapable of germination. The bearing of viability on effective dispersal is well illustrated by a study of the epidemiology of certain rusts. On the whole, uredospores are very resistant, and because they can survive for a long time in the air—resisting both desiccation and light—they can carry rust infection in a single step to a distance of a hundred miles and more. In contrast the smaller, thin-walled basidiospores (sporidia) are short-lived and are seldom capable of causing infection at a distance of more than a few miles from a source of infection.

The vast majority of fungi reproduce by spores, but some have reproductive units which cannot be classified as spores by any stretching of definitions. In the minute agaric *Omphalia flavida** (Fig. 3), for example, which causes a leaf-spot disease of coffee and many other plants in the New World, fruit-bodies are formed which liberate basidiospores in the normal way, but in addition reproduction occurs by means of multicellular macroscopic gemmae. Each of these appears to be homologous with a pileus, but

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* Buller (1934).

much smaller, and when ripe it becomes loosened from its stipe, is readily blown away, and, alighting on a suitable substratum, germinates to give a new mycelium. In *Sclerotium coffeicola*, another coffee parasite, reproduction and dispersal are entirely by gemmae which seem to be of the same nature as those of *Omphalia flavida*. Again, the sclerotium of ergot (*Claviceps purpurea*), like the host seed that it replaces, becomes detached from the host, and may play a part in dispersal although the spread of this fungus, under natural conditions, is mainly brought about by conidia and ascospores. However, the commonest type of this kind of vegetative reproduction occurs in lichens in which

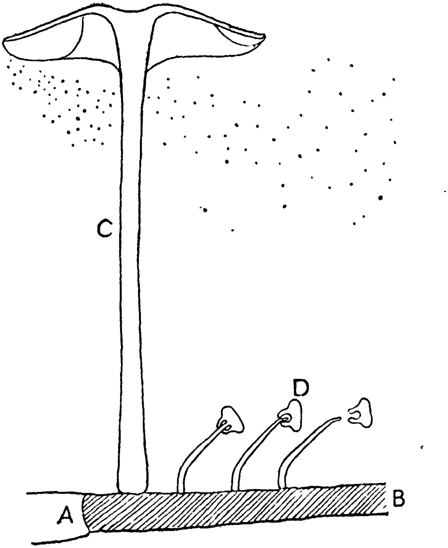

FIG. 3. *Omphalia flavida* parasitizing leaf of coffee.

Leaf tissue in vertical section: *A*, living; *B*, dead; *C*, sporophore liberating basidiospores; *D*, gemmifers each bearing a terminal gemma. *C* × 5, but *D* × 10. After figs. by Buller (1934).

reproduction by soredia is so frequent. In many lichens (e.g. *Cladonia* spp.) there occurs on the surface of thallus a dry, greyish powder each grain of which is a single soredium consisting of a tangled ball of fungal hyphae wrapped around a few algal cells. This powder is easily blown away by the wind. Many species rely for reproduction and dispersal entirely on soredia.

Further, somewhat as bracken spreads over the hill-sides by the growth of its underground rhizome, so a few fungi are dispersed locally by the growth of an underground rhizomorph. The most outstanding example is *Armillaria mellea*, the honey fungus. Basidiospores, carried perhaps from a considerable distance, establish the fungus as a saprophyte on a dead stump in a forest, but from there rhizomorphs grow out through the soil and attack living trees many yards from the base of operations.

Finally, a number of specialized parasitic fungi are dispersed by means of a resting mycelium carried by the reproductive unit, usually the seed, of the host plant. The most outstanding examples are the endophytes so commonly present in rye-grass (*Lolium perenne*) and its allies. These do not apparently sporulate in nature, but depend, with complete success, for dispersal on a mycelial infection of the seeds. The important problem of seed-borne fungi will be considered briefly in a later chapter.

It is often clear that the rate of spread of a fungus is conditioned by the efficiency of its dispersal apparatus. This can, perhaps, be illustrated most readily by a consideration of the two well-known potato diseases, blight due to *Phytophthora infestans* and wart disease caused by *Synchytrium endobioticum*. Blighted potato leaves bear, on their under surfaces, numerous conidiophores of *P. infestans* (Fig. 4) projecting through the stomata and bearing an abundant supply of the small conidia (sporangia) which are easily detached and scattered by the wind. This, combined with the speed of completion of the life-cycle, explains the epidemic spread of the disease when the weather is suitable. There are no practical steps that can be taken to control *dispersal* and the farmer can check the disease only by preventing infection, usually by spraying the foliage with Bordeaux Mixture before the spores of the pathogen become prevalent in the air. On the other hand, in *Synchytrium endobioticum* (Fig. 5), which attacks the underground parts, mainly the tubers, there are no air-borne spores. The short-lived zoospores discharged into the soil water are probably responsible for dispersal over a very short distance, at most a few feet, and the relatively large black resting-spores, liberated into the soil when the warted

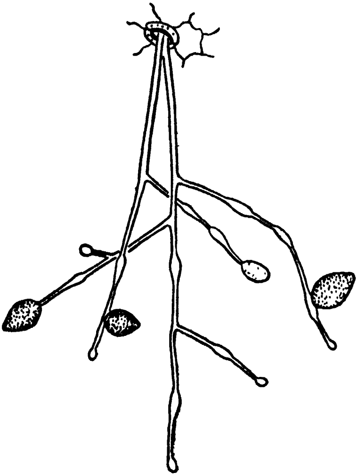

FIG. 4. *Phytophthora infestans*. Two conidiophores bearing conidia projecting through stoma on underside of potato leaf. Modified after Jones *et al.* × approx. 180.

tubers decay, are not normally dispersed by the wind. The disease may be spread by the transport of 'seed' potatoes carrying resting-spores from one area to another, by contaminated soil attached to the wheels of agricultural machines, and, more naturally but probably very occasionally, in infected soil on the feet of rooks and other birds. Thus the dispersal of the fungus can largely be prevented and its spread has been successfully limited by the measures adopted by the Ministry of Agriculture. The disease is notifiable, and susceptible varieties may not be grown in contaminated regions. Nor may tubers from an infected zone be transported to other regions and used as 'seed'.

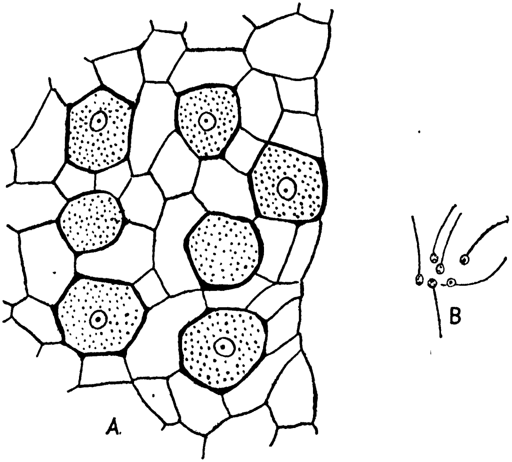

Fig. 5. *Synchytrium endobioticum.*
A, resting-spores in hypertrophied tissue of diseased potato tuber. *B*, zoospores. *A* and *B* × 300. After Curtis (1921).

In many fungi more than one kind of spore is produced in the course of the life-cycle, the rusts being, perhaps, the extreme example, with often five different spores (basidiospores, pycnidiospores, aecidiospores, uredospores, and teleutospores) in the cycle. Very often, where more than one kind of spore is formed they have different roles in dispersal. Thus in *Endothia parasitica*, causing the bark disease of American chestnut-trees, the ascospores, violently discharged into the air and readily distributed by the wind, are responsible for dispersal from tree to tree and from plantation to plantation, whilst the pycnidiospores, exuded in slimy masses from the pycnidia and washed down by the rain, are responsible only for the local spread of the disease on the trunk of the infected tree.

In most fungi the story of spore dispersal falls naturally into two episodes. First, spore liberation—the escape of the spores from immediate contact with the parent tissue—and this will be the subject of the next chapter. The second episode—the actual dispersal of the liberated spores by wind, insects, larger animals, splashing raindrops or running water—will be considered in later chapters.

II

SPORE LIBERATION

IN a great many terrestrial fungi the spores are violently discharged and are thus set free from the parent tissue, but in others liberation is passive so far as the fungus is concerned, and it is the energy of wind, rain, and animals that is responsible for the liberation of the spores and also, frequently, for their full dispersal.

Passive liberation

In the vast array of conidial apparatus exhibited by Hyphomycetes it has been suggested that one of the most fundamental biological distinctions is between 'dry-spore' and 'slime-spore' types.* Mostly, where the spores are dry they can readily be blown off their sporophores and carried away by the wind, whilst slime-spores are involved in a sticky liquid so that they cannot normally be dislodged by wind and appear to be dispersed, at least in the first instance, by water or by insects. A consideration of dispersal in Mucorales has led to much the same distinction† and the concept is clearly of general application in Fungi, so that most examples of passive spore liberation can be classed either as dry-spore or as slime-spore types, the former being the more numerous.

Amongst the larger fungi the most outstanding dry-spore forms are the puff-balls and their allies (*Lycoperdon* spp., *Geaster* spp., and *Scleroderma* spp.). An interesting but rather isolated example is the small agaric *Nyctalis asterophora*, which lives as a parasite on larger toadstools, especially *Russula nigricans*. In the parasite basidiospore forma-

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* Mason (1937).

† Dobbs (1939 and 1942).

tion on the greatly reduced gills is completely, or almost completely, suppressed and the whole upper surface of the cap is converted into a fawn-coloured, dry, powdery mass of stellate chlamydospores, easily blown away, which are the main units of dispersal. It is of interest to note that in the other common species, *Nyctalis parasitica*, the chlamydospores do not become powdery, and it is not at all clear how they are dispersed. The candle snuff fungus (*Xylaria hypoxylon*) is another common dry-spore fungus in which the white tips of the erect stroma are covered by minute powdery conidia readily scattered by the wind.

Amongst the micro-fungi many of the common saprophytes have dry spores, for example *Rhizopus nigricans*, *Penicillium* spp., *Aspergillus* spp., *Botrytis cinerea*, *Cladosporium herbarum*, *Monilia* (*Neurospora*) *sitophila*, *Alternaria* spp., and many more (Fig. 6). Anyone who has worked in a mycological or bacteriological laboratory knows to his cost that it is these dry-spore moulds which from time to time cause trouble as contaminants in cultures of other micro-organisms. However, mankind must be grateful for one such contaminant, for it was a spore of *Penicillium notatum* drifting by chance into a culture of bacteria that led Fleming in 1929 to his discovery of penicillin.

Amongst obligate parasitic fungi that spread with epidemic speed under suitable conditions, dry-spore types prevail, occurring, for example, in rusts (uredospore stage), in downy mildews and their allies (e.g. *Phytophthora infestans*), and in powdery mildews (oidial stage).

Although in most dry-spore fungi the spores are easily blown away by wind, sometimes their attachment to the sporophore is so firm that even the strongest winds fail to dislodge them. An outstanding example of this is the conidial (*Fusicladium*) stage of the apple scab fungus (*Venturia inaequalis*) in which wind alone does not seem to detach the spores, but in the presence of water they separate easily from their conidiophores and dispersal is, apparently, brought about in the main by wind-driven rain.* Even in highly developed dry-spore types, rain may play a part in spore liberation. Thus, in the puff-balls (*Lycoperdon* spp.) and earth-stars (*Geaster* spp.), wind blowing across the apical pore of the ripe fruit-body may suck out spore-laden air from within, but liberation of spores is brought about even more effectively by heavy rain, for when a large drop strikes the papery, waterproof peridium

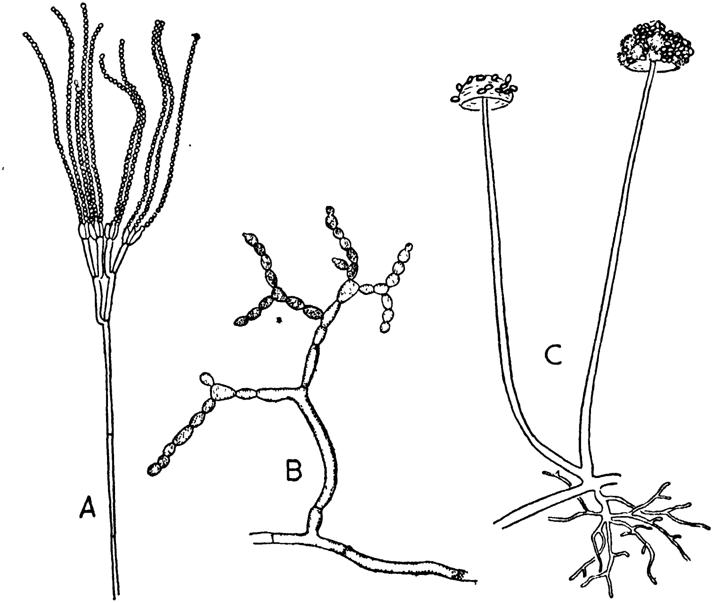

FIG. 6. Common dry-spore moulds.

A, Penicillium sp., × 280. *B, Neurospora (Monilia) sitophila,* × 250. *C, Rhizopus nigricans,* × 50

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* Frey and Keitt (1925).

the fruit-body is momentarily compressed and a visible cloud of spores is expelled.*

In the larger fungi there are few slime-spore forms, the most outstanding being the stink-horns (Phallaceae), but amongst micro-fungi numerous examples occur (Fig. 7).

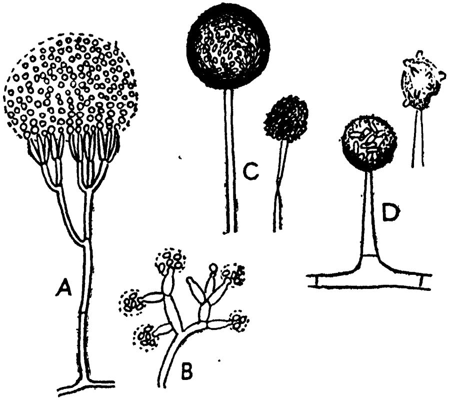

FIG. 7. Slime-spore micro-fungi.

A, *Gliocladium roseum*; *B*, *Trichoderma viride*. In *A* and *B* the slimy drops of spores are shown in sectional view; *C*, *Mucor racemosus*, sporangial drop in solid view under damp conditions (left) and after drying (right); *D*, *Coprinus fimitarius*, oidal fructification of monokaryotic mycelium in solid view under damp conditions (left) and after drying (right); *A*, modified after Mason (1937); *D*, after Brodie (1931).

Many soil fungi are of this type, for example: *Trichoderma viride*, *Mucor hiemalis*, *Fusarium* spp., *Pullularia pullulans*. Amongst plant pathogens the *Graphium* stage of *Ophiostoma ulmi* (the cause of Dutch elm disease), *Colletotrichum lindemuthianum* (causing anthracnose of dwarf and runner beans), and the conidial stage of ergot of rye (*Claviceps purpurea*) are familiar examples. Most pycnidial types have spores embedded in slime which exudes through the

* Gregory (1949).

ostiole as in the imperfect stage of *Endothia parasitica* (American chestnut bark disease) and in the pycnidial stage of rusts.

Active liberation. Ascomycetes

In some fungi the spores occur in or on a turgid cell which finally bursts, discharging the spores into the air. This type of active liberation is especially characteristic of the ascus of Ascomycetes. There are, however, many examples, widely scattered in any scheme of classification, in which the ascus is not explosive. Some would regard all such Ascomycetes as degenerate in this respect, but others would consider some genera primitive (e.g. *Endomyces*, *Monascus*, *Gymnoascus*) whilst agreeing that certain types with non-explosive asci (e.g. Tuberales, *Chaetomium* spp., *Ophiostoma ulmi*) are clearly degenerate in their ascus dehiscence. However, in the great majority of Ascomycetes, including lichens, the ascus is explosive and spore discharge is violent.

The typical ascus just before explosion is a turgid cell with the general properties of a thin-walled, living plant cell (Fig. 8). The thin, stretched, elastic cell-wall is freely permeable to water and to substances in true solution. However, the thin lining layer of enucleate protoplasm has the properties of a more or less semi-permeable membrane. These permeability relationships are indicated by the normal plasmolysis that occurs in an ascus if it is immersed in a hypertonic solution. In *Ascobolus stercorarius* it has been estimated that the osmotic pressure of the ascus sap is in the neighbourhood of 10–13 atmospheres.* The considerable stretching of the ascus that usually occurs as it ripens may be caused by an increase in the osmotic pressure of the cell-sap, due possibly to the conversion of reserve

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* Ingold (1939).

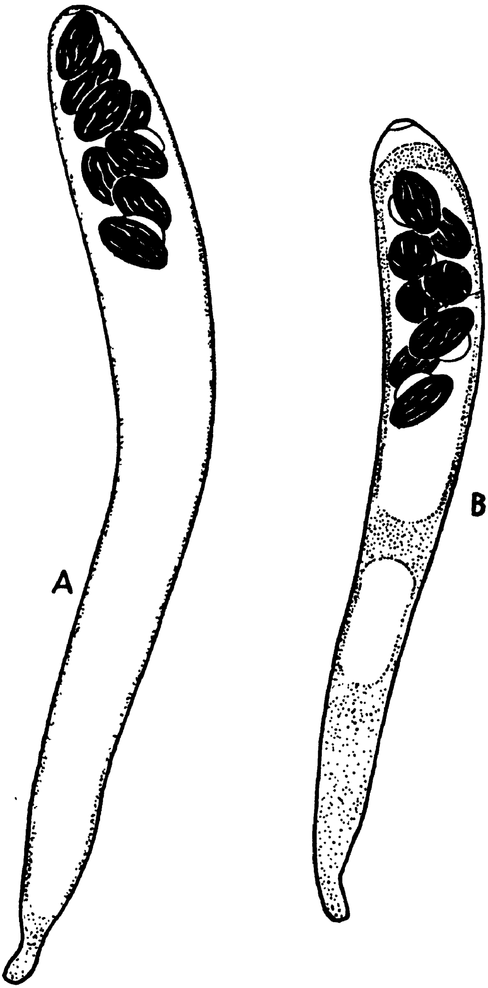

FIG. 8. *Ascobolus stercorarius.*

A, ascus mounted in water; *B*, ascus plasmolysed in 1·0 M cane sugar. In *B* the protoplasm is separating from the ascus wall at its tip. × 350.

glycogen to sugar, or to an increase in the extensibility of the cell-wall, or, perhaps, both these processes may contribute to the enlargement of the ascus. The ascospores occur suspended in the sap with the topmost spore at the apical end of the vacuole and, in some species at least (*Aleuria repanda*),* the spores are maintained in this position by a fine bridle of protoplasm. When the ascus bursts it does so in a definite manner: by a hinged lid in most operculate Discomycetes (Pezizales), by the separation of an apical cap (in *Dasyobolus immersus* and in *Sordaria curvula*), by the development of a minute apical pore as in Helotiales and Clavicipitales, or by an apical slit as in *Sphaerotheca*.

The ascospores in different species vary very considerably in size, shape, and in the distance to which they are discharged. This is in striking contrast to Basidiomycetes in which the size and shape of the basidiospores are subject to little variation from species to species and they are discharged to distances varying within narrow limits (0·01 cm.–0·10 cm.). Ascospores range in size from the huge spores of the lichen *Varicellaria microsticta* (up to 350 × 115 μ) to the minute ones (7 × 2 μ) of *Diatrype disciformis*, and in shape from the spherical spores of *Boudiera* spp. to the long thread-like ones of *Cordyceps militaris* (400 × 1·5 μ). Again, the distances of violent spore discharge range from 0·03 cm. in *Cordyceps militaris* to 60 cm. for *Dasyobolus immersus*. On the whole there is a correlation between the diameter of the spore-projectile and the distance to which it is shot.

In nearly all Ascomycetes complex sporophores or fruit-bodies occur, and in the larger forms a single fruit-body may produce millions of asci. It is easy to recognize four fairly distinct types of organization in connexion with spore liberation:

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* Buller (1909).

1. In the *Discomycete* type the spore-producing surface, consisting of asci intermixed with parallel paraphyses, is more or less exposed, most often as a lining to a shallow cup-shaped apothecium. The extensive exposed hymenium allows opportunities for 'puffing'—the simultaneous bursting of numerous asci.

2. In the *Pyrenomycete* type the asci are contained in a small flask-shaped structure (perithecium) which opens to the outside by a minute ostiole. Before each ascus can discharge the spores, its tip must reach the ostiole, and the canal of the neck is usually so narrow that normally only one ascus can emerge at a time.

3. In the *Erysiphales* type the fruit-body is a cleistocarp. This is rather like a perithecium but is completely closed; there is no ostiole. In this type the swelling asci must first burst the wall of the cleistocarp before they can emerge and discharge their spores.

4. In the *Myriangium* type, though the hymenium is exposed in a structure like a small apothecium, the spherical asci are embedded in a plectenchymatous tissue and are free to discharge only when this gradually undergoes gelatinization. Species of *Myriangium* and allied genera are nearly all fungi of warmer regions and are little known to British mycologists.

The first three types will now be considered in some detail.

Discomycetes

Discomycetes range from minute forms 0·2 mm. in diameter (e.g. *Saccobolus* spp.) to the large morels (*Morchella* spp.). Many are more or less cup-shaped with the hymenium lining the inside of the cup as in the genera *Peziza*, *Aleuria*, *Dasyscypha*, *Bulgaria*, *Helotium*, *Mollisia*; in others there is a more or less flat horizontal surface (e.g. *Rhizina*);

again, in some genera the hymenium is fully exposed on a stalked, club-like fruit-body as in *Geoglossum* and *Mitrula*; in the morels there is a stout, sterile stalk and the extensive hymenium is greatly convoluted, forming a series of broad alveoli or pits (Fig. 9).

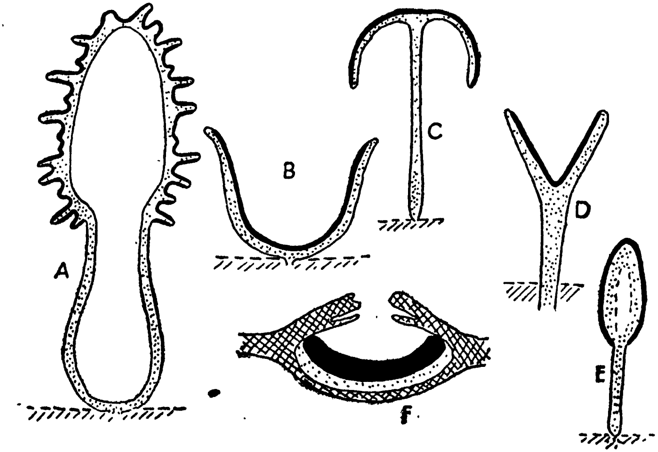

FIG. 9. Range of form of the apothecium in Discomycetes. Hymenium shown by thick black line. Soft fungal tissue dotted; sclerotial tissue cross-hatched. A, *Morchella rotunda*; B, *Aleuria vesiculosa*; C, *Leptopodia elastica*; D, *Sarcoscypha protracta*; E, *Mitrula phalloides*; F, *Rhytisma acerinum*.

The types of fruit-body architecture that have evolved seem to have depended on two main characteristics of the ascus: first, that its spores are usually discharged to a distance of 0·5–4·0 cm.; second, that the ascus is positively phototropic. A third point of importance is that the ascomycete hymenium is not apparently harmed by rain, in contrast to the hymenomycete hymenium which is completely disorganized by a film of water.

Since the ascospores are normally discharged to a distance of more than a centimetre, the spores, if shot vertically into the air, stand a reasonable chance of being blown away without falling back on to the parent hymenium. Consequently, the horizontal upward-facing type of hymenium is quite consistent with efficient dispersal and is, indeed, very frequently developed. The upward-facing hymenium hardly ever occurs in Hymenomycetes (toadstools, polypores, and their allies) where the basidiospores are rarely shot from the basidia to a distance of more than 0·02 cm. and where the hymenium is so susceptible to injury by water. On the other hand, the polypore or toadstool type of fruit-body, in which the vertical hymenial surfaces are closely opposed, could not have been developed in Discomycetes without a very considerable decrease in the violence of ascus discharge.

The phototropism of the ascus, originally recognized by Zopf in *Ascobolus*,* is probably a very common feature of the elongated type of ascus.† It has been reported in numerous genera, all belonging to the 'operculate' series, but probably it is of general occurrence. A hymenium lining a deep narrow cup, as in *Sarcoscypha protracta*, or the alveoli of such an elaborate fruit-body as that of *Morchella* spp., can function efficiently only because of this phototropism, for, as Buller has pointed out, if the asci were simply arranged at right angles to the general surface of the hymenium, a high proportion of discharged spores would be wasted by being flung against an opposing hymenial surface within range and directly in the line of fire of the asci (Fig. 13).

Spore discharge in the *Ascobolus* type of apothecium

Apart from its size *Ascobolus stercorarius* is fairly typical of a great many Discomycetes. This species is exceedingly common, growing in great numbers on horse-dung after

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* Zopf (1890).

† Buller (1934).

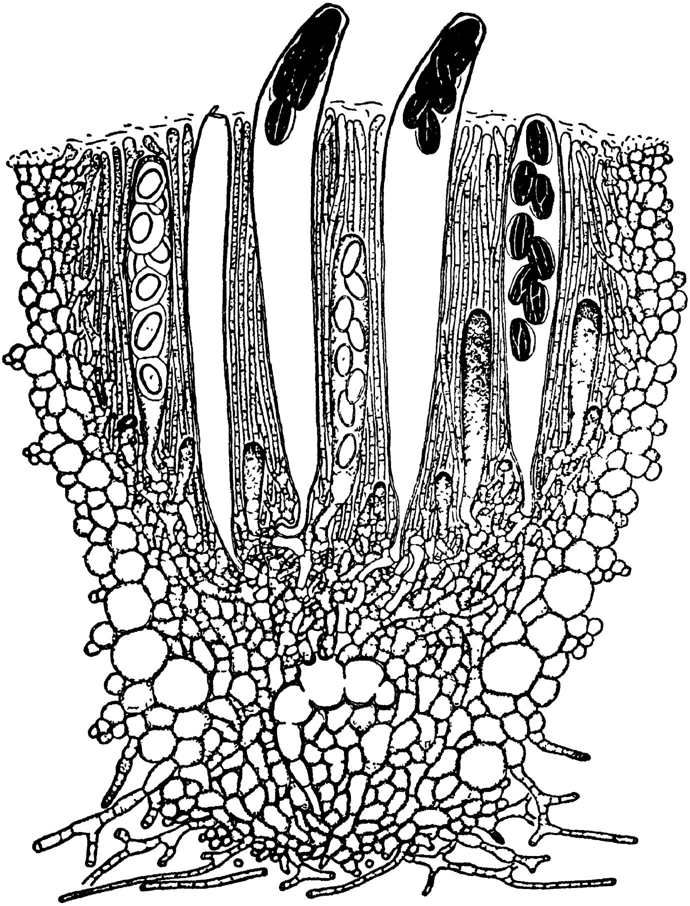

FIG. 10. *Ascobolus stercorarius*. Vertical section through apothecium. The projecting asci are pointing towards the incident light. After Corner (1929). × 216.

this has been kept in the laboratory for about two weeks. The apothecium is very small and the ripe asci project considerably beyond the tops of the paraphyses. The structure is illustrated by Corner's beautiful drawing* reproduced as Fig. 10. The apothecium, as in all Discomycetes, is composed of two intergrowing systems of hyphae: the ascogenous hyphae arising from the fertilized female organ (ascogonium) and producing asci at their extremities, and vegetative hyphae from below the ascogonium which form the bulk of the tissue of the apothecium including the walls of the cup and the long, narrow paraphyses which are intermixed with the asci. The hymenium, consisting of asci and paraphyses, is devoid of air spaces, for slimy material occurs between the hymenial elements and also spreads on the exposed surface of the hymenium as a thin layer penetrated only by the protruding tips of the ripe asci. Thus the hymenium has a characteristic 'water-soaked' appearance.

In *Ascobolus stercorarius* an apothecium remains active for perhaps ten days. Ripening of asci is periodic, a single crop of 20–40 maturing each day and discharging their spores about noon. The pigmentation of the spore-walls takes place late in development, so that the ripe asci are clearly distinguished from those that are one day younger not only by their greater length but also by having spores that are of a violet colour. Usually all mature asci discharge their spores simultaneously in a daily puff. This is a very striking phenomenon in the large species *Ascobolus magnificus*, in which the apothecia are 0·5–1·5 cm. in diameter. If the cover is removed from a fruiting culture of this species on horse-dung, the disk of each apothecium appears almost black, due to the dark spores in the projecting tips of hundreds of ripe asci. If the ripe apothecia are then breathed upon, their disks instantly change from

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* Corner (1929).

nearly black to greenish-yellow following the discharge of all the ripe asci.

In *Ascobolus stercorarius*, as in nearly all operculate Discomycetes, when the ascus bursts a small apical hinged lid is flung back, the stretched ascus-wall contracts longitudinally and transversely, and instantly the spores and some of the ascus sap are squirted into the air to a distance of several centimetres (Fig. 11).

It has been pointed out above (p. 21) that the phototropism of the asci in such a species as *Sarcoscypha protracta* permits the escape of spores that would otherwise be thrown against an opposite hymenial surface and so wasted. However, if there be a biological advantage in the phototropism of the asci in *Ascobolus*, it cannot be of this nature. Nevertheless, growing on an irregular surface such as the dung pellets of horse or rabbit, phototropism of the asci does help to ensure that the spores are thrown towards an open space away from the dung. This is clearly of some importance since successful dispersal in coprophilous fungi depends on the spores reaching the surrounding herbage.

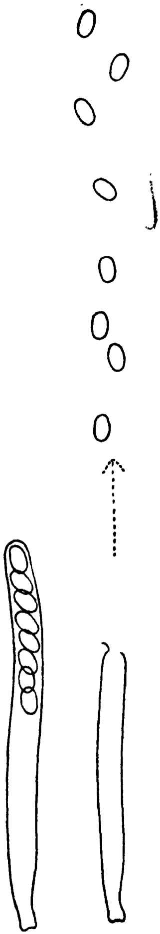

FIG. 11. *Pyronema omphalodes*. Ascus just before discharge and at the moment of discharge, × 250.

Spore discharge in the *Peziza* type

The most characteristic cup-fungi belong to the *Peziza* type, where the apothecium is relatively large (one to several centimetres in diameter) and distinctly cup-shaped. *Aleuria vesiculosa*, *Sarcoscypha coccinea*, *Galactinia badia*, and *Peziza aurantia* are well-known examples.

The organization of the apothecium in connexion with spore liberation has been the subject of careful study by Buller.* In *Aleuria vesiculosa* (Fig. 12) the apothecium is a deep cup lined by a hymenial layer containing millions of

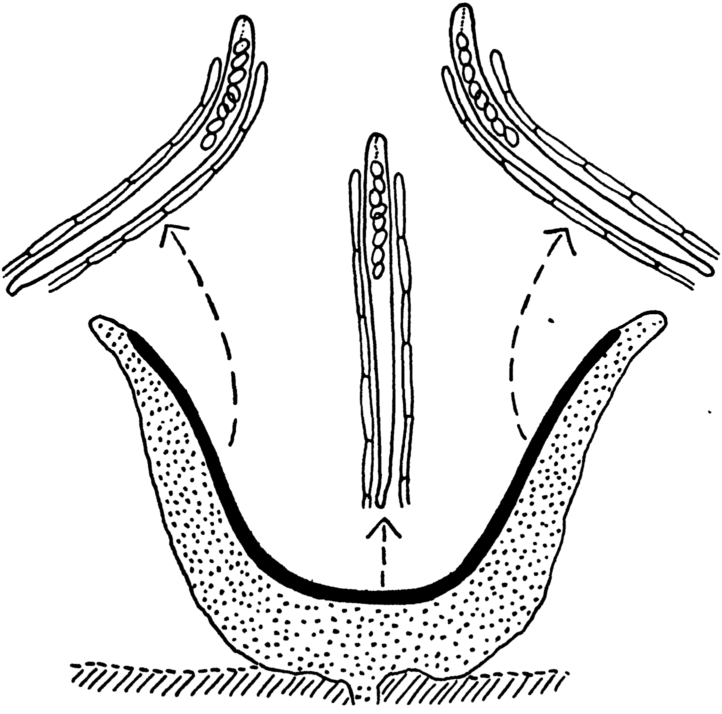

FIG. 12. *Aleuria vesiculosa*. Apothecium in vertical section. Hymenium shown black. An ascus and two paraphyses are shown taken from three indicated positions in the hymenium. Based on figures by Buller (1934). Apothecium × 4, ascus × 146.

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* Buller (1934).

asci intermixed with parallel packing filaments (paraphyses). All the elements of this layer are positively phototropic, and therefore point more or less towards the mouth of the cup. This condition where paraphyses as well as asci react to light is unusual and is known only in a few species. Because of this response, asci and paraphyses from the bottom of the apothecium are straight, but those from the more or less vertical sides of the cup are strongly curved. In *Aleuria vesiculosa* the eight ascospores form a single series in the ascus and are attached to its apex and to one another by a fine granular thread. When the ascus bursts a hinged lid flies back and the spores are squirted out to a height of 1–2 cm., the eight spores from one ascus being separated from one another in the air and not held together in a single mass. Buller* demonstrated this in a dark room by passing a strong beam of light above an apothecium from which spores were being liberated. The eight spores on discharge appeared 1–2 cm. above the hymenium as eight little motes spread out vertically at intervals of about 0·1 cm. in the beam of light.

In all these cup-fungi, as in *Ascobolus*, the eight spores appear to be discharged simultaneously from the ascus. However, it is likely that discharge in reality is successive, with an exceedingly minute fraction of a second elapsing between the liberation of sister spores, the interval being so small that to the eye discharge appears to be simultaneous. This theory is supported by the fact that the diameter of the ascus mouth is usually less than that of the spore, so that it is difficult to see how more than one could escape at a time. With the discharge of each spore the pressure in the ascus presumably falls, successive spores receive decreasing momenta, and are, therefore, shot to decreasing distances so that they become spread out vertically.

* Buller (1909).

The daily puff of spores in *Ascobolus* has already been considered, but the phenomenon of puffing is especially associated with the larger cup-fungi. During a period of quiescence thousands of asci reach a highly stretched condition of unstable equilibrium, so that the least shock —for instance a jerk, a sudden increase in temperature or illumination, or a change in humidity—is sufficient to cause all these asci to burst simultaneously, throwing into the air a visible cloud of spores that drift away like smoke. If a cup-fungus is picked and at once placed near the ear, puffing may occur and is then audible as a hissing sound. Once an apothecium has puffed it cannot, as a rule, be induced to do so again for a time, presumably because all the ripe asci burst at each puff. There is no doubt that puffing does occur under natural conditions, but it is not clear if it represents the usual method of spore discharge or whether, under field conditions, spore liberation may be more continuous, with only a few asci bursting at a time.

Falck,* in the course of his investigations of spore dispersal in Discomycetes, recognized two types. In the first, the *radiosensitive*, puffing does not occur, but spore discharge is greatly stimulated by incident radiation. *Morchella*, *Gyromitra*, *Helvella*, and *Geoglossum* are of this type. In the second, the *tactiosensitive*, puffing occurs in response to mild shocks, as when an apothecium is touched or blown upon. To this type most of the larger cup-fungi belong.

In *Aleuria vesiculosa* all the elements of the hymenium are phototropic, but this seems to be exceptional and usually response to light is limited to the projecting parts of the ripe asci, as in *Ascobolus*. This is so, for example, in *Ciliaria scutellata* and *Melastiza miniata*. In *Sarcoscypha protracta* (Fig. 13) there is no *evident* curvature even in the projecting parts of the ripe asci. Curvature does, however, occur

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* Falck (1948).

but is limited to the extreme tip, and the only result of this reaction to light is that the lid is displaced slightly towards the more strongly illuminated side of the apex, but this displacement is sufficient to direct the issuing ascus-jet towards the incident light.*

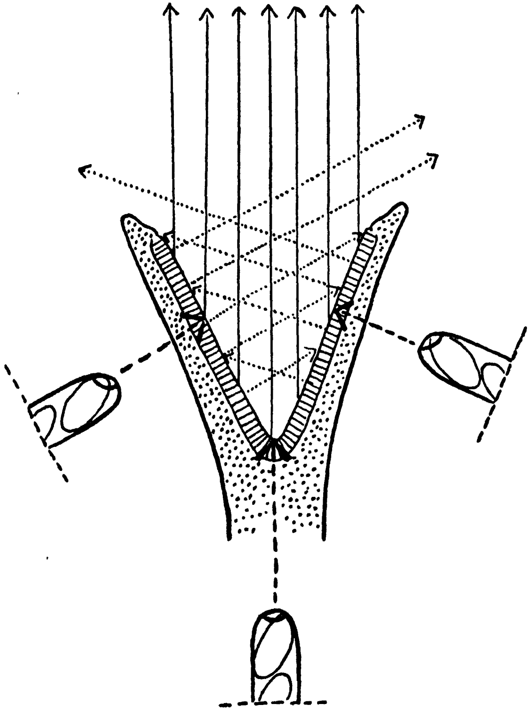

FIG. 13. *Sarcoscypha protracta*. Vertical section through apothecium. The projecting tips of three asci taken from three indicated places are shown highly magnified. Note the position of the lid in each. The solid lines with arrow-heads show the actual directions of spore-discharge. The dotted lines indicate the trajectories if the spores were discharged at right angles to the hymenium. Based on figures by Buller (1934).

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* Buller (1934).

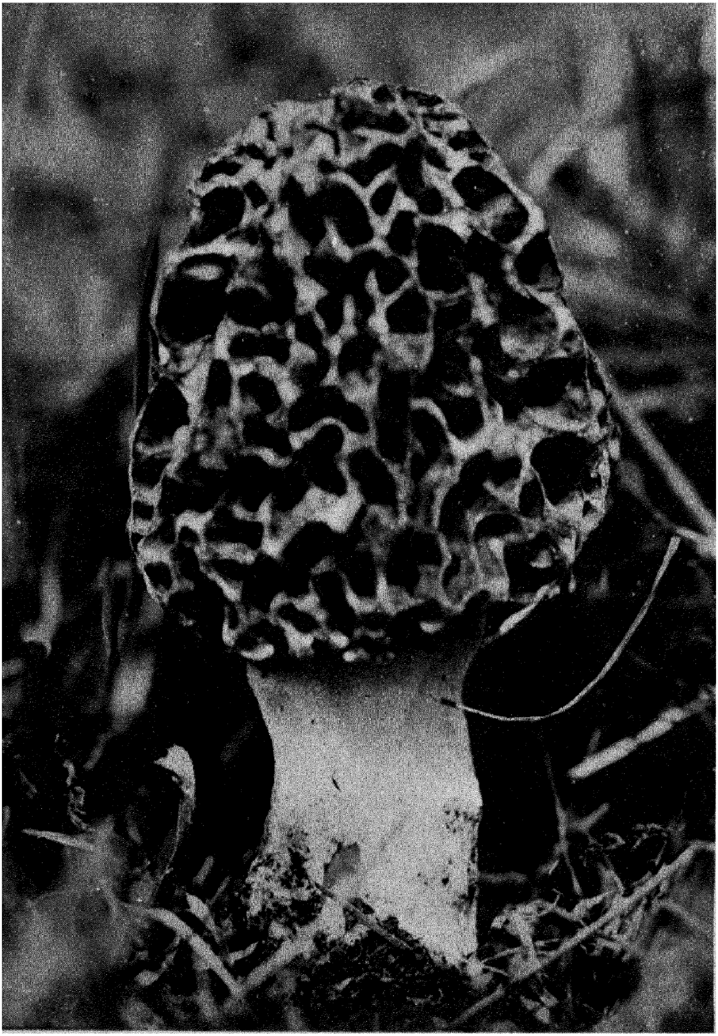

Photo E. K. Horwood

Plate I. Apothecium of *MORCHELLA ESCULENTA*

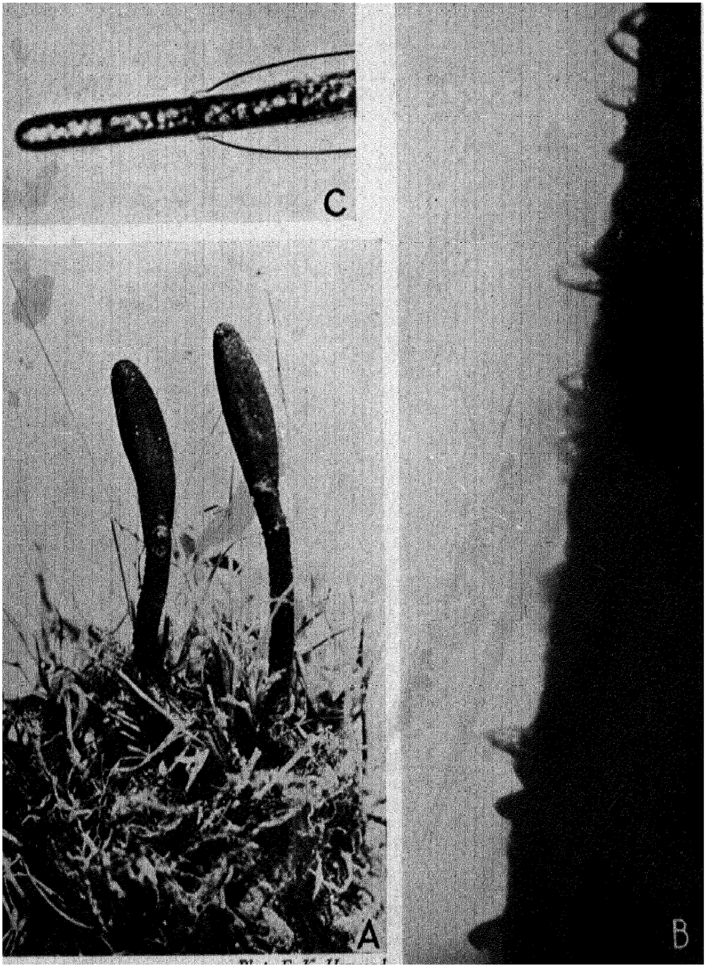

Photo E. K. Harwood

PLATE II. *GEOGLOSSUM OPHIOGLOSSOIDES*

A, two fruit-bodies; B, the edge of the fruit-body viewed under the low power of the microscope and showing the protruding tips of ripe asci; C, the tip of an ascus, seen under high power, showing one of the rod-like spores about to be shot away.

Sometimes, as in *Aleuria repanda*, the whole apothecium turns towards light, due to growth movement of the stipe, and in addition the individual asci are positively phototropic.*

Discharge in the *Morchella* type

The morels (*Morchella* spp.) have the most elaborate kind of apothecium (Plate I). There is a stout, sterile stalk and the spore-producing layer is spread over a surface consisting of a number of alveoli or shallow pits (Fig. 9 A). The hymenium of asci and paraphyses is continuous except for the exposed crests of the major ridges, separating neighbouring pits, which are sterile. The asci are phototropic and thus the escape of spores from the alveoli is assured.

Morchella has been regarded as the discomycete equivalent of *Boletus* in Hymenomycetes. Both have the hymenium lining pores, the striking difference in the size of these pores being associated with differences in the range of the ascus and the basidium. In *Morchella* it is the phototropism of the asci that determines the escape of the spores from the pits, which are, in the main, horizontal; in *Boletus* it is the positive geotropism of the downward-facing hymenial tubes that is so important, allowing the spores discharged into the middle of the tubes to fall freely until they reach the air below the pileus.

Successive discharge of ascospores in *Geoglossum*

In the examples considered above, all the spores of the ascus are liberated simultaneously or almost so. In sharp contrast are species of *Geoglossum* and *Trichoglossum*, in which the spores are shot from the ascus in definite succession.

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* Bayliss Elliott (1927).

The apothecium of *Trichoglossum hirsutum* or *Geoglossum ophioglossoides*, species quite often seen on lawns, is black, club-shaped, and 5–10 cm. high, with the hymenium covering the upper half of the club (Plate II). The hymenium has the usual organization, but the ascus contains a sheaf of eight long, septate ascospores (Fig. 14). When ripe it dehisces by the development of a minute apical pore. As soon as this is formed one of the spores is squeezed into it, completely stoppering the ascus. At first this spore is squeezed very slowly out of the ascus by the hydrostatic pressure within until about half of it is projecting. Then it rapidly gathers velocity and is finally discharged with such speed that its flight cannot be followed by the eye until, slowed down by friction with the air, it flashes into view about 0·5 cm. from the hymenium. Immediately following the discharge of one spore another takes its place, blocking the pore before the ascus can undergo any shrinkage. In its turn this spore is shot away a few seconds after the first, and so on until the whole complement of eight has been discharged. As soon as the last spore has been ejected the ascus suddenly contracts, since there is no longer a spore to act as a temporary stopper.

Pyrenomycetes

In Pyrenomycetes, the largest division of Ascomycetes, the asci are contained within a small flask-shaped structure (perithecium) rarely more than a millimetre in diameter. This opens by a narrow canal traversing the neck which may be very short (e.g. *Sordaria* spp.) or quite long (e.g. *Ceratostomella* spp.). Lining this canal are upward-projecting filaments (periphyses). For successful spore liberation the tip of the ascus must project beyond the mouth (ostiole) of the perithecium before it explodes. Owing to the narrowness of the neck-canal only one ascus can, as a rule,

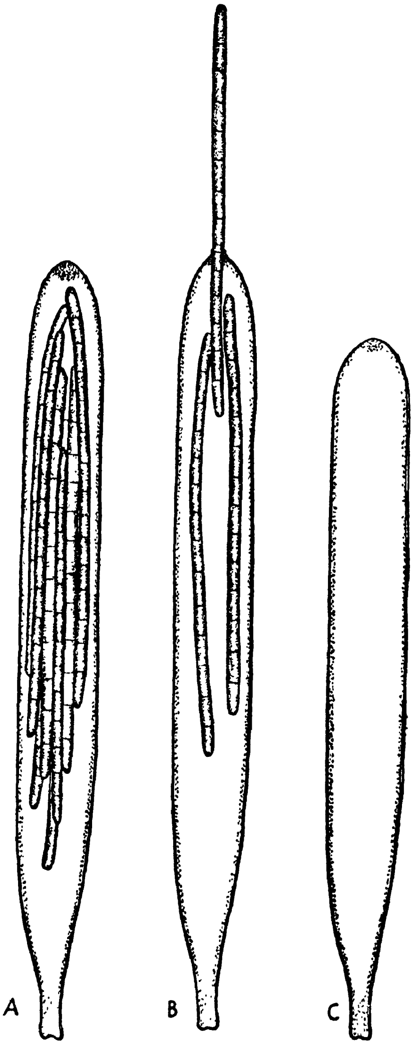

FIG. 14. *Trichoglossum hirsutum.*

***A*, mature ascus containing eight filamentous spores; *B*, a few seconds later, after five spores have been discharged; *C*, later still, after discharge of the eighth spore. × 380.**

reach the ostiole at a time, so that simultaneous bursting of asci, so characteristic of Discomycetes, cannot occur in Pyrenomycetes. In an active perithecium no gas-phase is present. Sometimes the asci, paraphyses, and periphyses are so tightly packed that there are no spaces between them, but if spaces do occur they are filled with slime.

Amongst Pyrenomycetes several more or less distinct types of spore discharge can be recognized and will now be considered in turn.

Sordaria type

For watching spore discharge the small Pyrenomycetes that appear with such regularity on the dung of herbivores are especially favourable.* This is particularly true of the two very common and closely similar species *Sordaria curvula* and *S. tetraspora*. In most Pyrenomycetes the wall of the perithecium is quite opaque, but in these two species it is semi-transparent, so by focusing an optical section the behaviour of the living asci can be seen in a specimen mounted in water (Fig. 16). Most of the asci occur crowded in the lower half of the perithecium attached to a basal cushion of tissue, but the upper half is occupied by the greatly swollen upper parts of those asci that are fully mature. Between the perithecium wall and the mass of asci are very thin-walled, much-inflated cells of the paraphyses. The top of the perithecial cavity tapers and finally merges into a short, narrow canal leading to the outside. One of the mature asci in the upper region of the perithecium is usually slightly in advance of the others, and if this is watched it may be seen to elongate, in part probably due to actual growth and in part to the pressure of surrounding turgid cells. Finally the tip of the ascus reaches

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* Ingold (1933 and 1939).

the ostiole and protrudes very slightly beyond it. It then explodes, discharging a projectile, consisting of the ascus cap, eight spores bound together by ropes of mucilage, and some ascus sap, to a height of about 20 cm. On discharge

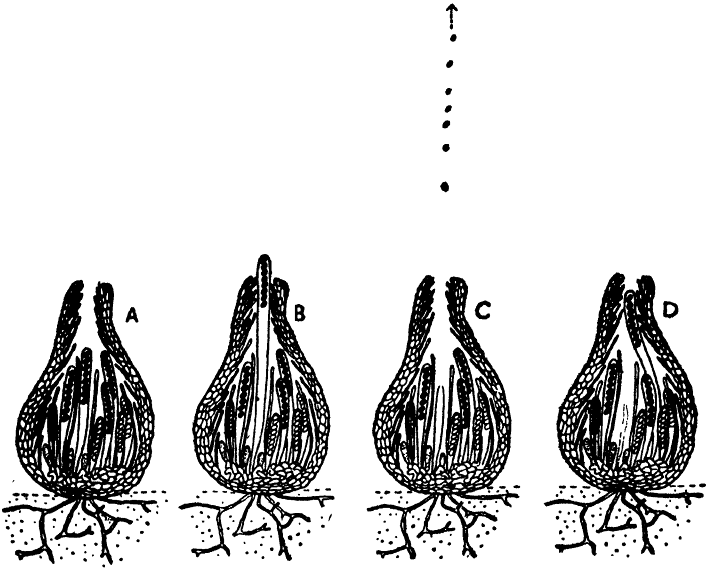

FIG. 15. Diagram of discharge in *Sordaria* sp.

A, the tip of an ascus is just entering the neck-canal of the perithecium; *B*, a few minutes later, the tip now protrudes through the ostiole; *C*, the next instant, the ascus has burst and the empty envelope has retracted into the perithecium; *D*, some minutes later, the old empty ascus is breaking down and another ascus is elongating up the neck-canal.

the elastic wall of the ascus, which is enormously stretched but still attached to the interior of the perithecium, retracts into the perithecium, where it soon disintegrates. As soon as one ascus has discharged, another begins to elongate up the neck, and so the process goes on in orderly succession.

One interesting feature of *Sordaria*, also found in a

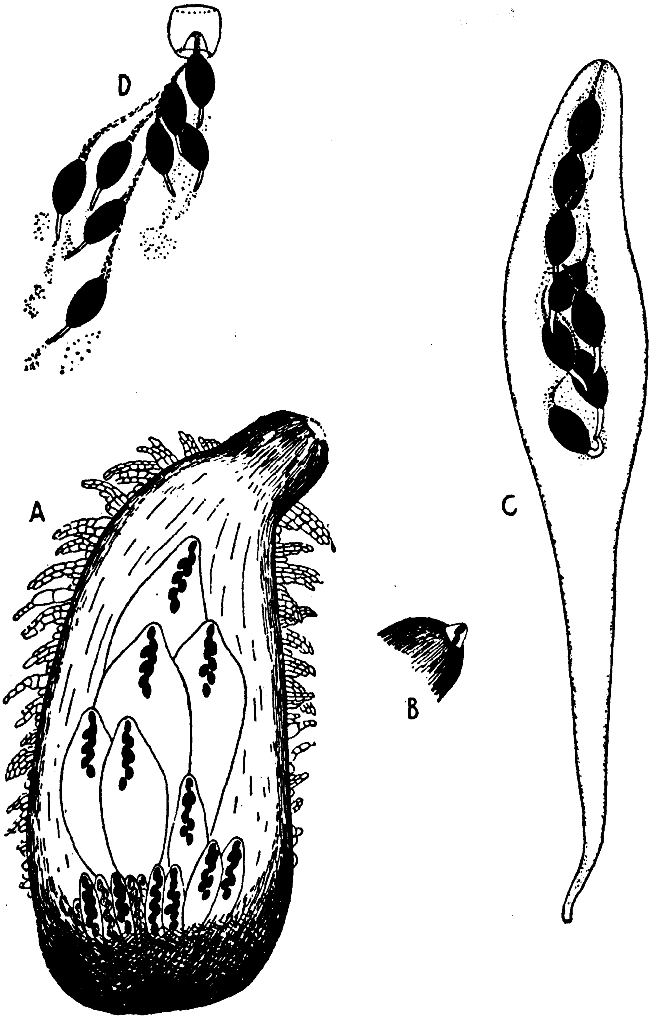

FIG. 16. *Sordaria curvula.*

A, perithecium with the asci showing through the semi-transparent wall; *B*, ostiole region of the same perithecium ten minutes later—the tip of the leading ascus in *A* has now reached the outside and is about to discharge its spores; *C*, a single ascus which has just commenced to swell; *D*, a discharged spore-mass showing the ascus cap, partly turned inside out, attached to the apical spore. *A* and *B* × 83, *C* and *D* × 270.

number of allied genera, is that the neck of the perithecium is positively phototropic (Plate III).

The essential features of the *Sordaria* type are, first, that the ascus remains attached to the basal cushion inside the perithecium, and second, that it reaches the outside by elongation involving the gradual stretching of the whole ascus wall.

Sporormia type

The distinctive feature of this type is that the ascus has a double wall. This is a fairly common type frequently noted and figured since it was first described by Pringsheim* in *Pleospora scirpicola*. A common example is *Sporormia intermedia* (Fig. 17), a frequent member of the horse-dung flora. The asci occur attached to a basal cushion within the perithecium, but each has a jack-in-the-box construction. The ascus wall consists of an outer relatively thick and fairly rigid membrane and an inner thin, extensible one. Shortly before discharge, the outer membrane is ruptured apically and, the wall pressure being now reduced, the ascus is free to absorb water, with the result that it elongates very rapidly up the neck-canal of the perithecium and soon projects through the ostiole. The ascus then bursts, squirting its spores simultaneously into the air.

Leptosphaeria acuta (Fig. 18†), a very common saprophyte on the dead stalks of nettle, agrees in general with *Sporormia*, but the spores (as in *Geoglossum*) are discharged in succession through an apical pore.

In the double-wall type of ascus a curious and apparently constant feature is the enormous swelling of the thin inner wall that occurs immediately after discharge, due, no doubt, to the absorption of water. This swelling was clearly

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* Pringsheim (1858).

† Hodgetts (1917).

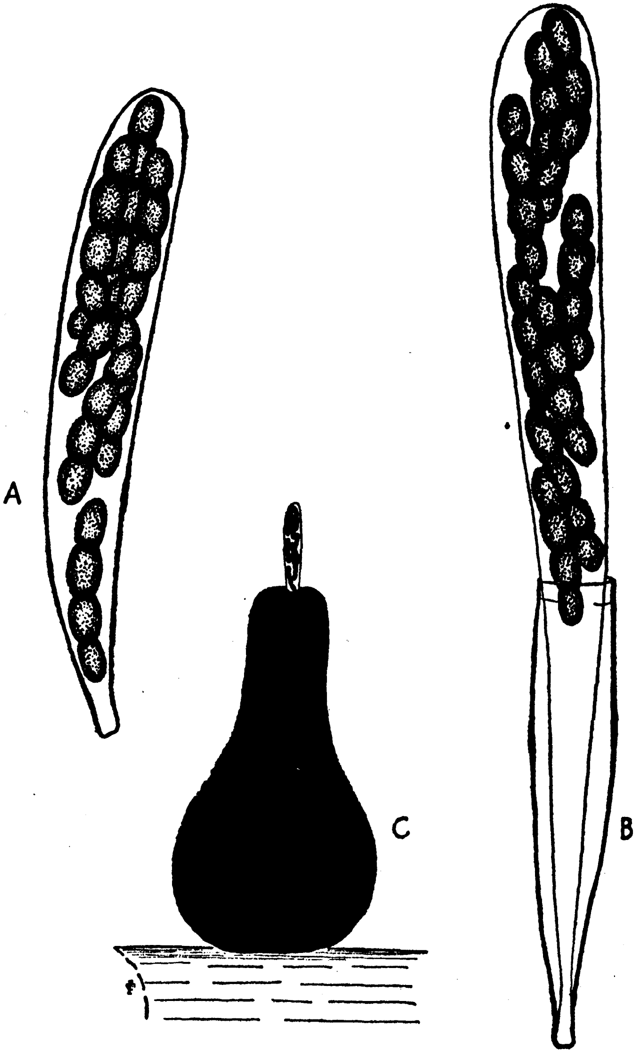

FIG. 17. *Sporormia intermedia.*

A, ascus before rupture of outer wall, × 700; *B*, another ascus after rupture of the outer wall and elongation of the inner wall, × 700; *C*, perithecium, on piece of straw on horse-dung, with ascus tip protruding, × 124.

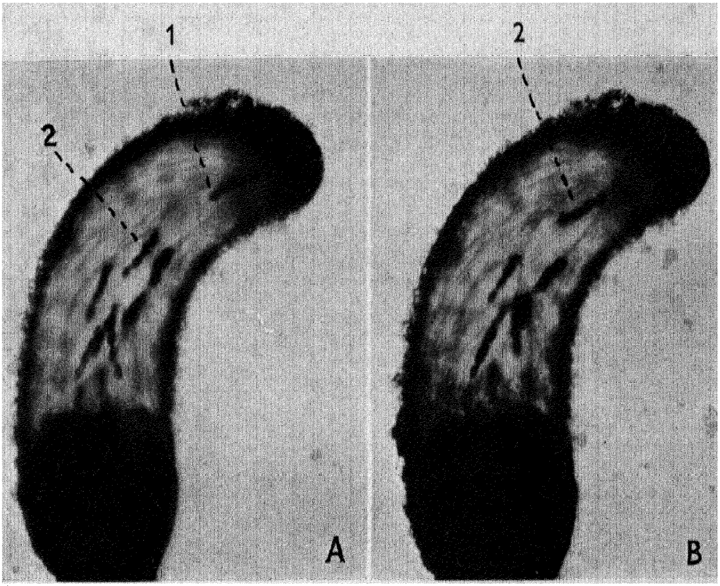

PLATE III. *SORDARIA TETRASPORA*

A, living perithecium mounted in water and seen in optical section. The tip of ascus no. 1 is nearing the ostiole; B, the same, 25 minutes later. Ascus no. 1 has discharged its contents and ascus no. 2 is now elongating towards the ostiole. The fungus has developed in a dish lighted from one side and the phototropic neck of the perithecium is pointing towards the light. × 462.

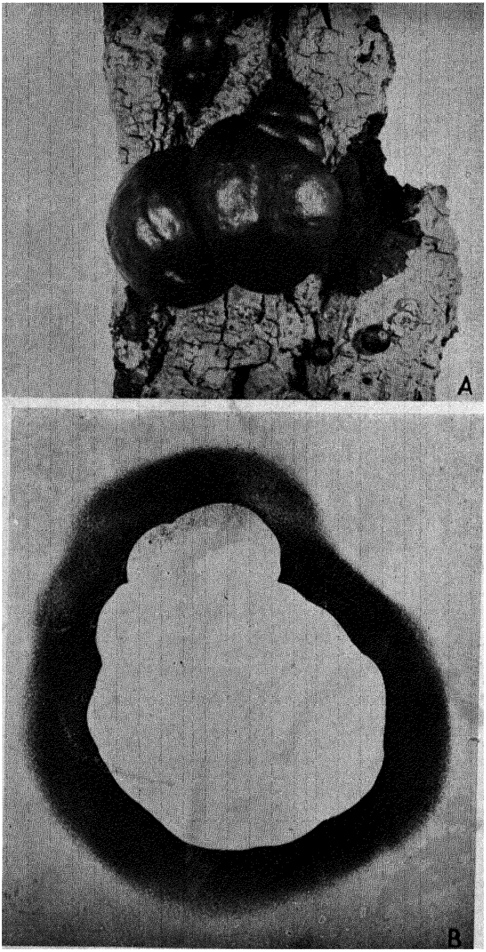

Photo C. E. B. Dobb

PLATE IV. *DALDINIA CONCENTRICA*

A, piece of ash-bark, bearing smallish perithecial stromata. B, black deposit of discharged spores produced overnight around a perithecial stroma; before taking the photograph the stroma was removed, and its position is represented by the central white space. A and B both natural size.

illustrated by Pringsheim* when he described this kind of discharge nearly a hundred years ago (Fig. 19).

Cordyceps type

Spore discharge in *Cordyceps militaris* is rather similar to that in *Leptosphaeria acuta*, but there are some interesting points of difference. *C. militaris* is a common parasite of the larvae and pupae of Lepidoptera. From the dead, mummified pupa in the soil, orange, club-shaped stromata grow above the ground. The upper parts of these stromata bear numerous reddish-orange perithecia, partly projecting as conical pimples. Spore discharge is easy to see in this fungus and the spores are so long that the process can be watched under a lens. In *C. militaris*, and in the Clavicipitales generally, the ascus is very long, narrow, and cylindrical and the wall consists of a single layer. The tip of the ascus is characteristically thickened and on dehiscence is pierced by a narrow, tubular pore. The spores are very long and

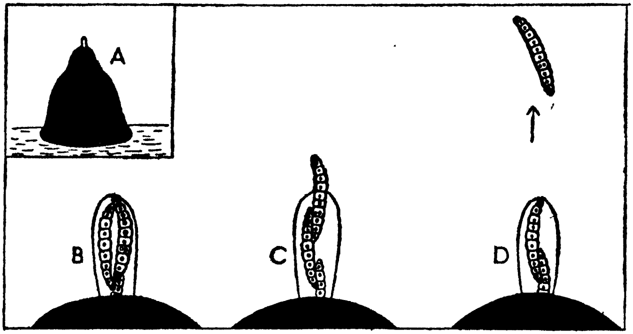

FIG. 18. *Leptosphaeria acuta*.

A, perithecium with tip of an ascus protruding; *B–D*, apex of perithecium showing successive spore discharge from protruding ascus. *A* × 8, *B–D* × 200. Slightly modified after Hodgetts (1917).

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* Pringsheim (1858).

extremely narrow, forming a sheaf of eight, and, as generally happens with long, narrow spores, they are discharged in obvious succession. On watching an active perithecium under the high power of a miscroscope, the tip of an ascus suddenly appears at the ostiole and elongates rapidly until it is protruding to the extent of 40–60 μ (Fig. 20). Then suddenly an ascopore flashes into sight about 200 μ from the ostiole and quickly sinks out of view. Then, a second or two later, another appears, and so on. After each spore is discharged the ascus may retract by a few microns and may or may not elongate again before the next spore is discharged. Between the liberation of sister spores some fluid contents are seen to ooze out of the ascus and flow down

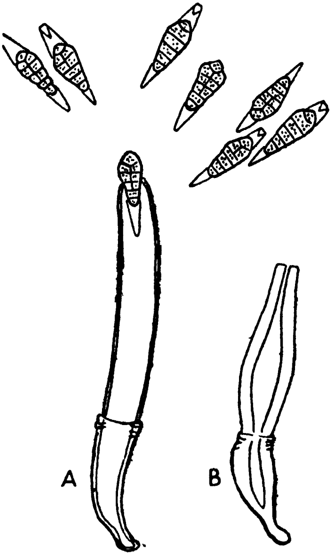

FIG. 19. *Pleospora scirpicola.*
A, Ascus in the act of discharging its eighth spore; the seven other spores are seen outside; *B*, empty ascus immediately after discharge of the eighth spore. After Pringsheim (1858).

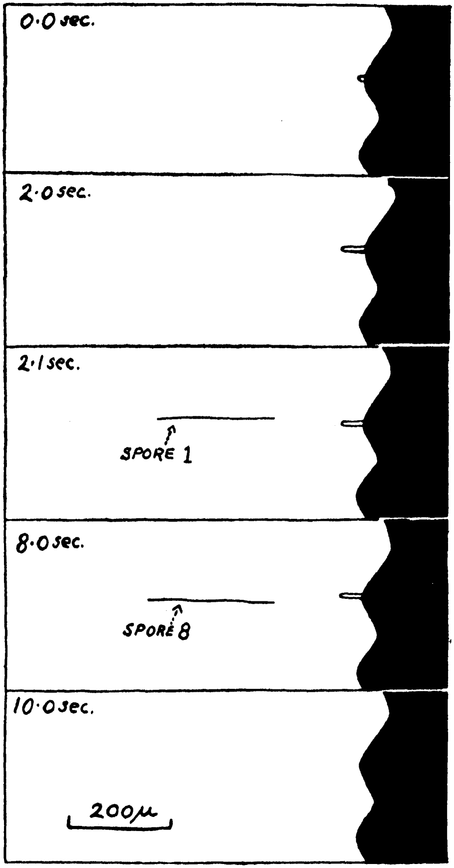

FIG. 20. *Cordyceps militaris*. Two projecting perithecia as seen when stroma is laid on its side.

At 0·0 sec. the tip of an ascus is beginning to project from an ostiole. At 2·0 sec. the projecting tip has reached its maximum length. At 2·1 sec. the first spore flashes into view and then rapidly falls out of sight. At 8·0 sec. the last spore has been discharged. At 10·0 sec. the empty ascus has retracted into the perithecium.

its outside. As soon as all eight spores are discharged the empty ascus collapses. Then, after an interval varying from half a minute to ten minutes, another ascus protrudes and discharges its spores.

The most curious feature of discharge in *Cordyceps* is that the spore leaves the ascus at such speed that nothing is to be seen of it until it flashes into sight about a quarter of a millimetre from the ostiole; at no stage is it seen protruding from the ascus and stoppering it as in *Geoglossum* or as in *Leptosphaeria acuta*. It is difficult to understand how the long, thread-like spore can reach sufficient speed within the ascus so as to leave it without being visible to an observer. In *Epichloe typhina*, another member of the Clavicipitales, spore discharge is much as in *Cordyceps militaris*, but the interval between the liberation of successive spores is very small and usually the escape of all eight spores occupies less than a second. Sometimes a spore follows its predecessor so rapidly that its apex sticks to the base of the first and a long filament consisting of several spores end to end may then be discharged in one piece.

Detached-ascus type

This type is found particularly amongst long-necked species of Pyrenomycetes. It has been described in *Endothia parasitica*, *Gnomonia rubi*,* and *Ceratostomella ampullasca*.† In this last species (Fig. 21) the perithecium is immersed in rotting oak wood with only the tip of the neck projecting. Within the perithecium the asci arise from a basal cushion but they break free when mature. The flask thus becomes filled with many thousands of small asci, mostly detached. These absorb water, and a pressure develops within the perithecium which is relieved by the asci passing out in single file through the narrow neck-canal. In *Ceratostomella*

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* Dowson (1925).

† Ingold (1933).

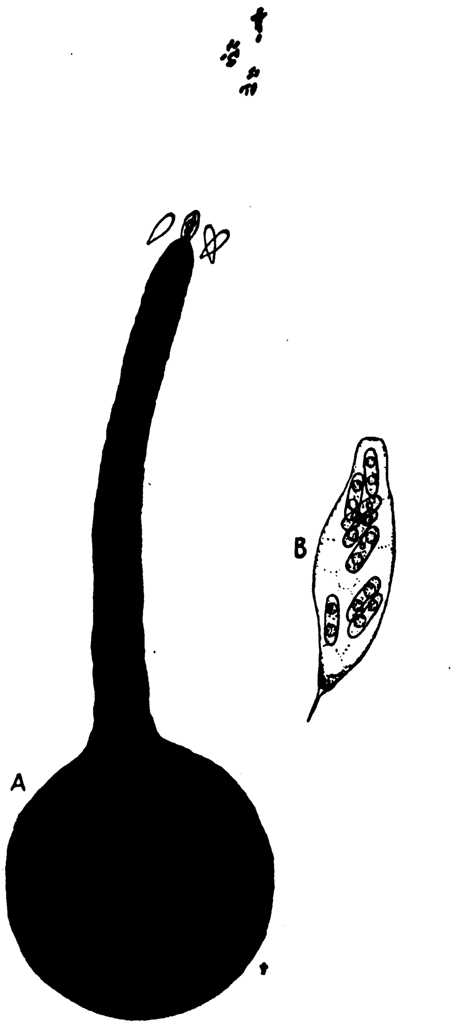

FIG. 21. *Ceratostomella ampullasca.*

A, perithecium mounted in water with an ascus at the ostiole about to discharge its spores. Three empty asci are seen near the ostiole. The three groups of spores discharged from these are shown; *B*, a single mature detached ascus. *A* × 65, *B* × 500.

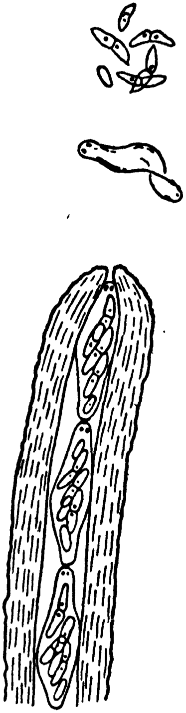

FIG. 22. *Gnomonia rubi.* Neck of the perithecium in optical longitudinal section showing passage of asci along neck-canal. Above the ostiole the spores and empty membrane of a discharged ascus are shown. After Dowson (1925). × 450.

the neck is opaque and the actual movement of the asci in the canal cannot be observed, but in *Gnomonia rubi*, due to the transparency of the neck, this movement can be seen (Fig. 22).

In *Ceratostomella* there is a narrow, slit-like ostiole, and when an ascus reaches this it pushes the slit wider open and protrudes until the spore-containing part is exposed. At this stage the lower part of the ascus is still held by the lips of the ostiole. The ascus then bursts, scattering its spores. Immediately afterwards the empty ascus is pushed out by the one below, and so on. This may be a very quick-firing mechanism with only a few seconds elapsing between successive ejections.

This detached-ascus type represents a mechanism of discharge which allows rapid spore liberation from a long-necked perithecium. It is clear that had each ascus to elongate from the basal cushion up a neck-canal 1–2 mm. in length, spore discharge would certainly be slow.

Non-explosive types

In a number of Pyrenomycetes the asci are no longer explosive. Their walls deliquesce within the perithecium and the liberated spores form a mass intermixed with mucilage. This absorbs water, swells, and oozes out through the ostiole, like tooth-paste out of a tube, often forming a tendril-like thread composed of innumerable spores. This type of spore liberation is characteristic of the large genus *Chaetomium* (Fig. 23) and occurs also in some species of *Ceratostomella*. In *Daldmia concentrica*, which grows so abundantly on dead ash-trees, violent spore discharge is the rule, but at times the normal mechanism fails and spore-tendrils are produced. They are not, however, formed in quite the same manner as in *Chaetomium*.* An ascus elongates and nearly reaches the ostiole, but instead of bursting explosively its contents

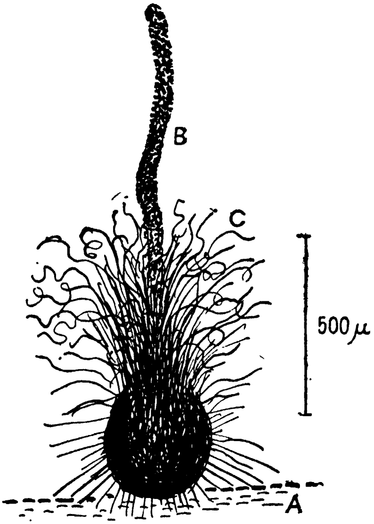

FIG. 23. *Chaetomium cochliodes*. Perithecium growing on filter-paper (A).

A spore-tendril (*B*) has been produced, but its point of origin is obscured by the curly hairs (*C*) that cluster thickly around the ostiole.

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* Bayliss Elliott (1920).

merely ooze out. The next ascus behaves likewise and piles its eight spores just behind the first eight, pushing them forward a trifle. As the process goes on the spore-tendril grows longer and longer. Spore-tendrils or spore-horns are also a feature of the pycnidial stage of many Ascomycetes. Thus in *Diatrype stigma*, so common on beech bark, the pycnidia exude orange tendrils several centimetres in length and it is these that are the most conspicuous feature of the fungus at this stage of its life-history.

Spore output by perithecia

The perithecium of Pyrenomycetes is always a small structure and is not subject to the great range of size-variation seen in the apothecia of Discomycetes. This is very understandable, for in Pyrenomycetes discharge is normally limited to one ascus at a time and, therefore, increase beyond a certain size is of no value. Perithecia of different species do, however, vary considerably in their spore-liberating capacity, as may be seen from Table I, which gives the rate under favourable conditions of spore discharge from perithecia of a number of species.

TABLE I

Species	*Estimated spore-output per perithecium per hour under favourable conditions*	*Reference*
Sordaria minuta . .	24	Griffiths (1901)
S. curvula . . .	40	Ingold (1933)
Sporormia intermedia .	184	,, ,,
Hypoxylon coccineum .	1,800	,, ,,
Diatrype disciformis .	23,000	,, ,,
Endothia parasitica .	14,000	Rankin (1914)

Conditions affecting spore discharge in Pyrenomycetes

The principal conditions that affect spore discharge in the Pyrenomycetes are the supply of water, temperature, and light.

Since violent spore discharge involves the bursting of turgid cells, it is clear that a supply of water is essential if it is to go on. The majority of Pyrenomycetes have hard, resistant perithecial walls or have their perithecia immersed in hard stromatal tissue. Most can be air-dried without injury, and this is true even of some fleshy forms (e.g. *Nectria cinnabarina*). They are essentially drought-resisting xerophytes which, however, discharge their spores only during wet periods when the fungal tissue is fully turgid. This has, for example, been clearly demonstrated for *Endothia parasitica*,* the cause of American chestnut blight, in which the ascospores are ejected into the air only during rain and so long as the bark remains wet. From March to October discharge occurs during each spell of rain. Observations on the apple scab fungus†

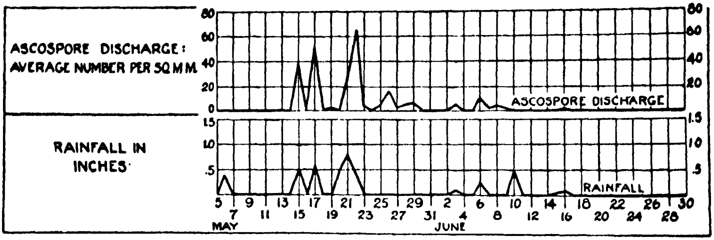

FIG. 24. *Top*: graph of discharged ascospores caught on glass slides arranged a few millimetres above fallen apple leaves bearing perithecia of *Venturia inaequalis* in an orchard; ordinates give daily catch in spores per square millimetre of slide surface. *Bottom*: graph of daily rainfall. After Keitt and Jones (1926).

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* Heald and Studhalter (1915).

† Keitt and Jones (1926).

(*Venturia inaequalis*), which discharges its ascospores from perithecia developed on the old fallen leaves in spring, show a close correlation between periods of rainfall and periods of spore discharge (Fig. 24). In some species* (e.g. *Hypoxylon pruinatum*) it has been shown that a saturated atmosphere is not sufficient to initiate spore discharge, but that the perithecial stroma must first be wetted before discharge will begin.

Daldinia concentrica is a special kind of xerophyte† able to continue spore discharge during dry periods by virtue of a considerable reserve of water in the stromatal tissue. This fungus is very common on dead ash branches (Plate IV) and is to be found on other trees that have been scorched by fire. The fungus is usually somewhat hemispherical and often about the size of half an apple. The surface layers of the stroma are extremely hard and resistant, and no doubt the nature of this tissue helps in reducing loss of water by evaporation. The very numerous perithecia occur immersed in this peripheral tissue. The bulk of the stroma is composed of tissue showing the curious concentric zoning from which the specific epithet is derived (Fig. 25).

A single stroma lasts only for one season, and the perithecia ripen and begin to shed their spores in May and may continue to do so until September. During this period discharge is not dependent upon rain but on the water reserve of the stroma. An active specimen gathered in early May has a density of just over 1·0, but as the water reserve is exhausted the density falls. If an active stroma is brought into a dry room and left fully exposed without any extraneous water-supply, spore discharge will continue for weeks. Even when placed in a desiccator with the air kept bone dry by anhydrous calcium chloride, discharge may

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* Gruenhagen (1945).

† Ingold (1946).

go on for many days. It is only when evaporation has led to the reduction of the density of the stroma to less than 0·3 that spore discharge finally ceases. In its water relations *Daldinia* is rather like a cactus. It is a succulent xerophyte.

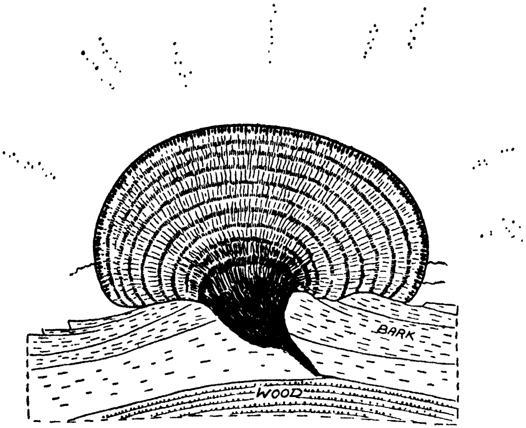

FIG. 25. *Daldinia concentrica.* Section through perithecial stroma; the black dots just within the surface are the perithecia. Spores are shot to a distance of 1·5 centimetres. Nat. size.

Another interesting example* of a stromatal pyrenomycete that is not directly dependent on rain for its spore discharge is *Epichloe typhina* (Fig. 26), which occurs commonly on a large number of grasses, especially *Dactylis glomerata*, *Holcus mollis*, and *Agrostis tenuis*. The orange perithecial stroma is produced in July and August as a conspicuous crust around the grass-shoot just above a node. Immersed in the stromatal tissue are numerous perithecia from which long, thread-like spores are violently discharged. If a stroma is held in the hand with sunlight

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* Ingold (1948).

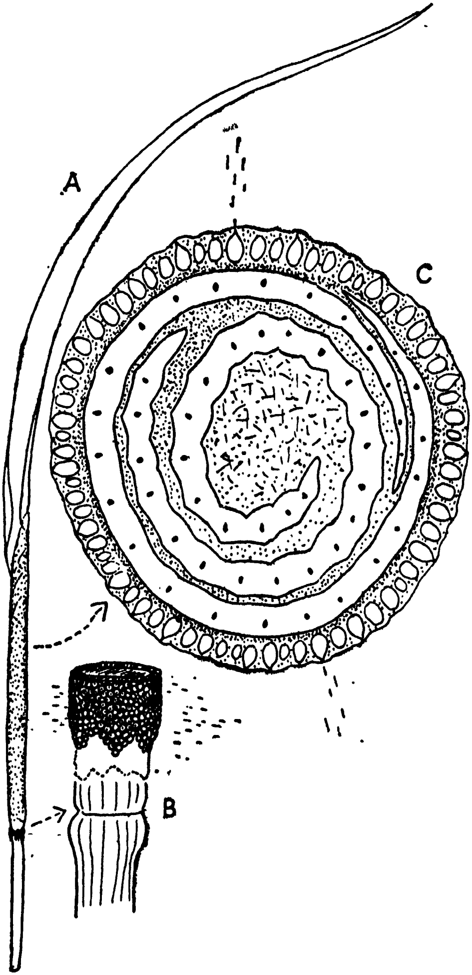

FIG. 26. *Epichloe typhina.*

A, shoot of *Dactylis* with perithecial stroma above node; *B*, details of region just above node; *C*, *T.S.* showing stroma with perithecia. Fungal tissue is dotted; leaves shown white with vascular bundles as black dots. In *B* and *C* discharged spores are shown in the air around the stroma. *A* × 0·5, *B* × 4, *C* × 20.

falling on it from just the right direction, the escaping spores can be seen with the unaided eye. Spore discharge is not dependent on external water, and if a stalk of grass bearing a stroma is brought into a dry room, discharge continues for days, provided that the cut end of the grass stalk is in water or, in other words, that the transpiration stream of the host is maintained. If this stream is interrupted, spore liberation from the fungus soon ceases. In this species the water for spore discharge is clearly being derived from the living tissue of the host.

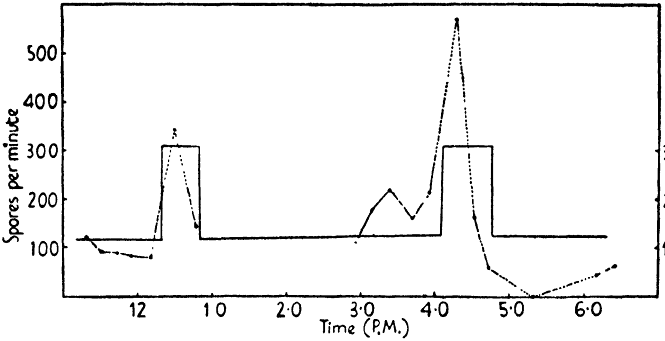

FIG. 27. Spore-output of a perithecial stroma of *Hypoxylon coccineum.*

The stroma was kept on damp blotting-paper, on which it had been resting for some days before the experiment, and was kept in the dark. The solid line indicates the temperature. Points on the dotted line represent rates of spore output.

Concerning the effect of temperature on spore discharge little information is available. Below 5° C. discharge is probably arrested in most species. Above 5° C. and below 35° C. a rise in temperature tends to increase the rate of spore liberation. A record of spore ejection from a perithecial stroma of *Hypoxylon coccineum* at a low temperature (13–15° C.) and after transferring to a relatively high one (32° C.) is reproduced in Fig. 27.* The result of a change

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* Ingold (1939).

from the lower to the higher temperature is a sudden increase in the rate of spore output which, however, rapidly falls off.

A study of the daily march of spore ejection has demonstrated in most species examined a periodicity governed, in all probability, by the periodic changes in illumination that occur as night follows day. Some species are essentially nocturnal in the spore liberation (e.g. *Daldinia concentrica** (Fig. 28) and *Hypoxylon fuscum*) whilst others are diurnal (*Nectria cinnabarina* and *Sordaria curvula* (Fig. 29)).† The whole question of the cause of this periodicity is in need of careful experimental study.

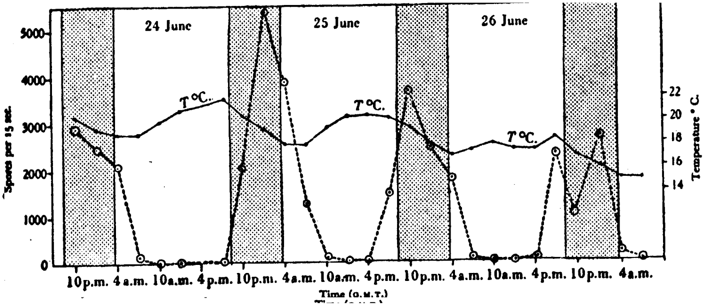

FIG. 28. Spore discharge in *Daldinia concentrica*. Interrupted line: rate of spore discharge as spores caught in fifteen seconds on a square cm. of glass surface held just above a large stroma. Continuous line: temperature. Periods from sunset to sunrise stippled.

Spore liberation from the cleistocarps of powdery mildews and from the ascus of *Protomyces*

In Erysiphales (powdery mildews) the cleistocarp (cleistothecium) is like a small perithecium, but without an ostiole. It is essentially a hibernating structure which remains dormant throughout the winter, but shows the

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* Ingold (1946).

† Ingold (1933).

renewed activity in spring that eventually leads to the discharge of the ascospores. Within the firm wall of the cleistocarp one or several oval asci occur. In some species only the ascospores are violently ejected; in others the asci are first shot away and then burst, scattering the spores.

Sphaerotheca mors-uvae is an example of the first type.[*] The single ascus within the cleistocarp swells in the spring, and this leads to the rupture of the cleistocarp wall by a slit through which the ascus protrudes as it continues to swell. Finally the ascus bursts and the ascospores are squirted out (Fig. 30).

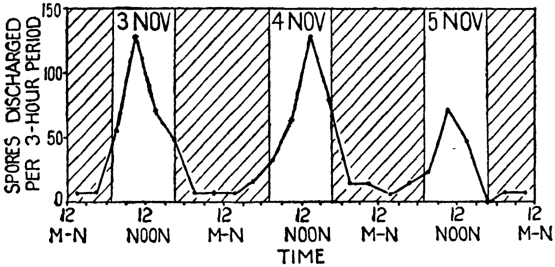

FIG. 29. *Sordaria curvula.* Continuous record of spore discharge from a perithecium for three days. Periods from sunset to sunrise hatched. Experiment performed in thermostated greenhouse with temperature varying between 18° and 20° C.

In *Podosphaera leucotricha*[†] double discharge occurs. This has been observed by Woodward and is best described in his own words:

> The perithecium is a true cleistocarp, the ascus being ejected through an irregular rupture of the wall. The opening formed gradually widens owing to the expansion of the ascus following the absorption of water. . . . The perithecial wall is elastic and

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[*] Salmon (1914).

[†] Woodward (1927).

responds to the pressure exerted from within until the opening, although small in diameter, can no longer retain the ascus which squeezes through the orifice and is violently ejected. The force of ejection is considerably increased by the snapping together of the 'jaws' of the orifice, due to the elasticity of the perithecial case. . . . The ascus is often thrown several centimetres in the air. On reaching water or in a damp atmosphere, it continues to swell and within one or two minutes explodes, scattering the ascospores in all directions.

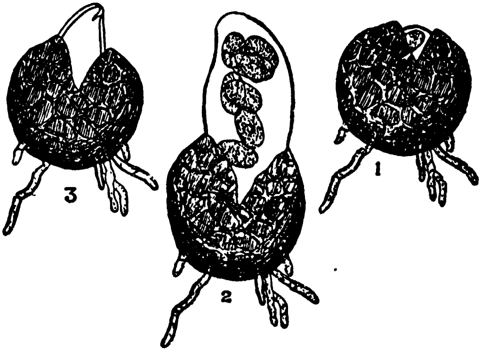

FIG. 30. *Sphaerotheca mors-uvae.* Discharge of ascospores. 1, swelling ascus is just bursting cleistocarp-wall; 2, fully swollen ascus is about to discharge its spores; 3, an instant later. After Salmon (1914).

Spore discharge in *Protomyces* may be considered at this point because it resembles, somewhat, discharge in *Sphaerotheca. Protomyces* is one of those unfortunate genera which have failed to settle neatly into any scheme of classification. Some have placed it in Phycomycetes as an archimycete type; others have tried to push it into Ustilaginales; others, in despair, have made for it a special group of fungi, Protomycetes; but now most mycologists are resigned to including it amongst the 'lower' Ascomycetes.

Species of *Protomyces* occur as obligate parasites on herbaceous plants, but are of no economic importance. *P. macrosporus* on *Aegopodium*, *P. pachydermus* on *Taraxacum*, and *P. inundatus* on *Apium nodiflorum* are common species. They produce small warts on the stalks and veins of the leaves and on the stems. Each wart is the result of a single infection and, in section of a wart, the fungus is seen as an intercellular mycelium of limited extent with many much-enlarged intercalary 'chlamydospores' each with a two-layered wall. These are resting spores in *P. macrosporus* and *P. pachydermus*, but in *P. inundatus* they germinate at once. When fully developed, the warts on *Apium* split open exposing the parasite. Each exposed 'chlamydospore' may be regarded as an ascus confined within an outer rigid cell-wall. As the cell absorbs water the ascus expands, bursts through the outer rigid cell-wall and lies free as a spherical cell containing a large number of minute spores clumped together (Fig. 31). The ascus then bursts by a slit and the spores are thrown into the air to a distance of about 2 cm.

Spore discharge by water-squirting in Phycomycetes

There are apparently few examples of fungi discharging their spores by a water-squirting mechanism outside Ascomycetes, although possibly discharge of basidiospores in Basidiomycetes may turn out to be of this nature. In Phycomycetes there are, however, three rather isolated but interesting examples: *Pilobolus*, *Basidiobolus*, and *Empusa*.

Pilobolus

Species of *Pilobolus*, a genus of Mucorales, develop with great regularity and in abundance if freshly deposited horse-dung is kept in the light under a bell-jar, and may also frequently be seen on dung in the field, especially under the humid conditions of early autumn. The commonest species are *P. kleinii* and *P. longipes*. There is a diurnal periodicity, conditioned by light,* in the development of the crops of ripe sporangiophores which usually mature and discharge their sporangia round about noon.

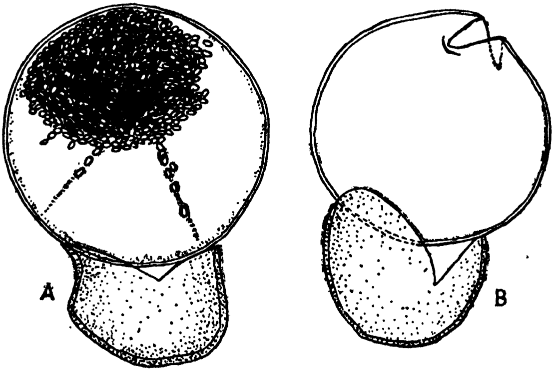

FIG. 31. *Protomyces inundatus.*

A, just before discharge; the ascus has burst free from its outer thick wall and has swollen considerably; *B*, after discharge, showing the empty ascus. × 320.

The structure of the asexual apparatus in *Pilobolus* is fundamentally like that of *Mucor* (Fig. 32), but differs in one notable feature, the presence of cross-walls separating the sporangiophore from the feeding mycelium.

The sporangium (Fig. 33) is bounded by a wall which is relatively thick and blackened in its upper regions, but thin and transparent below. Within are numerous spores occupying the upper part of the sporangium, and below them is a ring of mucilage encircling the columella.

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* Buller (1934); McVickar (1942).

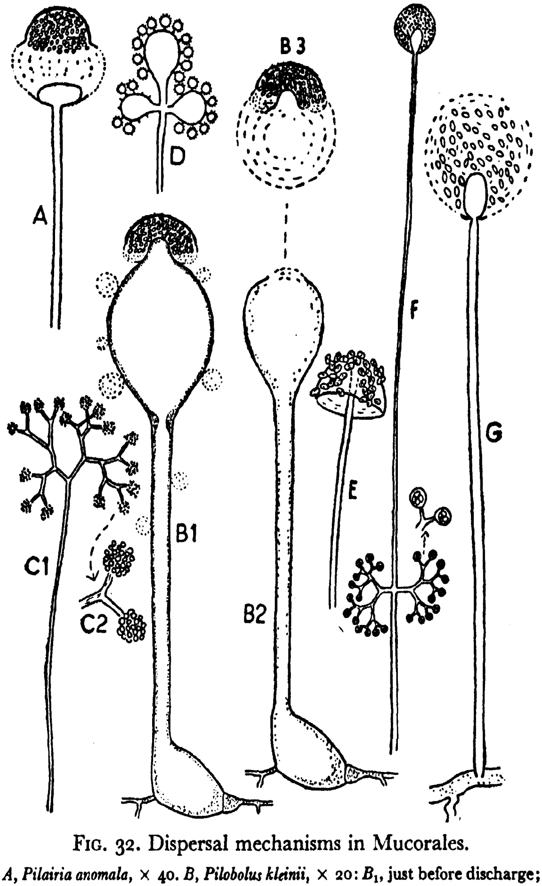

FIG. 32. Dispersal mechanisms in Mucorales.

A, *Pilairia anomala*, × 40. *B*, *Pilobolus kleinii*, × 20: B_1, just before discharge; B_2, sporangiophore; and B_3, projectile at moment of discharge. *C*, *Sporodinia grandis*: C_1, sporangiophore, × 15; and C_2, two sporangia, × 50. *D*, *Cunninghamella elegans*, conidiophore, × 100. *E*, *Rhizopus nigricans*, dry-spores on collapsed columella, × 80. *F*, *Thamnidium elegans*, sporangiophore with terminal sporangium and lateral sporangioles, × 10. *G*, *Mucor hiemalis*, sporangiophore with sporangial drop, × 25.

Shortly before the sporangium is discharged its wall ruptures along a transverse line of weakness in the transparent region so that the sporangium gapes open there, exposing the mucilage.

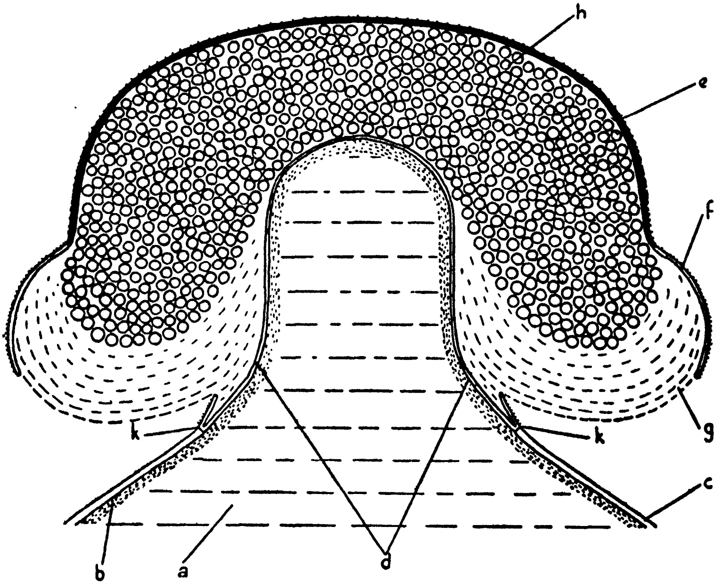

FIG. 33. *Pilobolus longipes*. Diagram of dehisced sporangium just before discharge.

a, sporangiophore sap; *b*, lining layer of protoplasm; *c*, wall of sporangiophore; *d*, columella; *e*, black part of sporangium wall; *f*, transparent part of sporangium wall; *g*, mucilage; *h*, spores; *k*, region where sporangiophore ruptures.

The sporangiophore is a single cell composed of a basal bulb that is more or less buried in the substratum, a straight stalk part, and a subsporangial bulb the apex of which bulges into the sporangium as a substantial columella. There is a thin lining layer of protoplasm, but where the subsporangial bulb meets the stalk this layer is thicker and more conspicuous, being coloured orange by innumerable oil drops containing a carotinoid pigment. Within the protoplasmic layer of the sporangiophore is a large vacuole filled with cell-sap having an osmotic pressure of some 5 atmospheres.* The ripe sporangiophore is a highly turgid cell covered with numerous minute droplets of fluid presumably exuded under the influence of the hydrostatic pressure within (Plate V).

There is a circular transverse line of weakness in the sporangiophore just below the junction of the sub-sporangial bulb with the columella (Fig. 33). Finally, rupture occurs along this line and the stretched sporangiophore wall contracts, squirting out a drop of sap that carries the sporangium, including the columella, to a height of 50–200 cm. The sporangium wall, like the back of a duck, cannot be wetted. The ring of mucilage below the spores is, however, very readily wettable, as is also the inner surface of the columella, with the result that the sporangium projects partially from the drop of sap with which it is associated. When the projectile strikes an object, although the sporangium may be momentarily submerged by the accompanying drop of sap, it bobs up to the surface of the drop with the unwettable wall outwards. As the drop dries, the ring of mucilage comes in contact with the surface of the object and finally dries to a hard cement, so that the sporangium is firmly stuck with the spores completely covered by the black sporangium wall.*

It is interesting to notice in passing the wide variety of spore-liberation types in Mucorales—a very natural order of Fungi (Fig. 32). *Pilobolus* is the only genus with violent spore discharge. In most species of *Mucor* the sporangiospores are slime spores. Thus in *M. hiemalis* and *M. racemosus* when the sporangium is ripe its wall dissolves (it

* Buller (1934).

is said to be diffluent) and becomes converted into a sporangial drop.* When this dries the spores are firmly cemented to the columella and cannot be dislodged by wind. Just how they are dispersed is not at all clear—perhaps it is by rain splash. The same type of sporangial drop is found in the beautiful *Phycomyces blakesleeanus*—a fungus of great value to the botanist and to be found in every botanical laboratory, but little known in nature. *Phycomyces* has xerophytic features. If it is grown on nutrient agar in an open petri dish freely exposed in a desiccator containing anhydrous calcium chloride, sporangiophores are produced as readily as in damp air and grow to the same considerable length (10–15 cm.), and at their ends the usual slimy masses of spores are produced. This unique xerophytism of *Phycomyces* is due in part to the chitinized wall of the sporangiophore and in part to the freedom with which water streams into the sporangiophore, making good any loss by evaporation. *Pilaria* is a curious genus with a sporangium structure exactly like that of *Pilobolus*, but with a sporangiophore of the *Mucor* type. *Pilaria anomala* is very common on horse-dung, developing just before the *Pilobolus* crop. There is a straight and, at first, short sporangiophore terminated by the sporangium, which splits, as in *Pilobolus*, by a transverse line of weakness, exposing the mucilage within. Then the phototropic sporangiophore elongates enormously and very rapidly, often carrying the sporangium on to the surrounding herbage, to which it becomes firmly cemented like a discharged sporangium of *Pilobolus*.† *Rhizopus nigricans*, black bread-mould, is a typical dry-spore fungus. When the ripe sporangium is exposed to dry air its wall cracks into numerous small pieces and exposes, on the collapsed columella, a mass of dry, powdery spores which are easily

* Dobbs (1939).

† Ingold (1939).

blown away. A very similar example is *Sporodinia grandis*, common on decaying agarics in autumn. Here the sporangiophore is dichotomously branched. Each sporangium has an excessively thin wall. This breaks down completely at maturity, exposing the dry, powdery spores. *Cunninghamella elegans* is another example of a highly successful dry-spore mechanism. In this species swollen heads of conidia are produced instead of sporangia. These conidia are finely attached and easily blown away. *Thamnidium elegans* is of special interest. It produces a long sporangiophore with a large terminal sporangium of the *Mucor* type which finally becomes a sporangial drop, but in addition short but much-branched laterals from the sporangiophore bear minute sporangioles, each containing a small number of spores, usually four. These sporangioles when ripe readily break off and can be dispersed by wind.*

Basidiobolus

Basidiobolus ranarum (Fig. 34) occurs with great regularity on the excrement of frogs, the conidiophores projecting into the air looking like minute specimens of *Pilobolus* (Plate V). The conidiophore arises from a single cell of the septate mycelium or directly from a discharged conidium. There is a straight stalk and a sub-conidial bulb, the tip of which projects as a minute columella into the spore. The conidiophore is a highly turgid cell which finally bursts along a transverse line of weakness near the base of the bulb, not near the top as in *Pilobolus*, and the elastic part of the stretched wall is above this line, not below it. Thus, on bursting, the stretched elastic wall of the upper part of the bulb contracts, squirts sap backwards, and flies off on the recoil carrying the conidium with it. It is a minute water rocket.† During the flight through the air

* Ingold (1940).

† Ingold (1934).

the two parts of the projectile usually separate so that, although the conidium is shot to a distance of 1–2 cm., the accompanying portion of the conidiophore (the 'basidium') is rarely thrown farther than 0·5 cm.

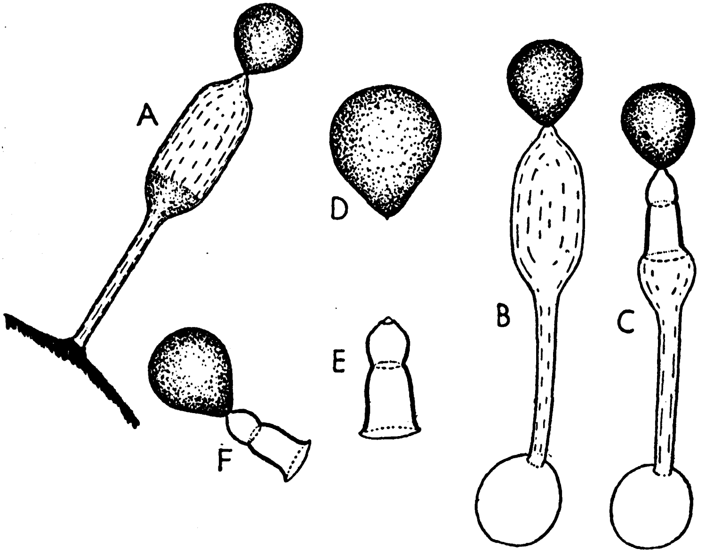

FIG. 34. *Basidiobolus ranarum.*

A, mature conidiophore growing on natural substratum; *B*, living conidiophore derived directly from a conidium mounted in water; *C*, the same after the addition of a trace of iodine; *D*, a discharged conidium; *E*, a discharged 'basidium'; *F*, a conidium and 'basidium' which have failed to separate in mid-air. *A*, *B*, and *C* × 410; *D*, *E*, and *F* × 520.

Empusa muscae

House flies are frequently seen in the late summer attacked by *Empusa muscae* (fly cholera) (Fig. 35). Just before death a doomed fly, plugged with the fungus, usually attaches itself to some object, often a pane of glass, by its sucker-like proboscis. Then in a few hours thousands of conidiophores protrude between the segments of the

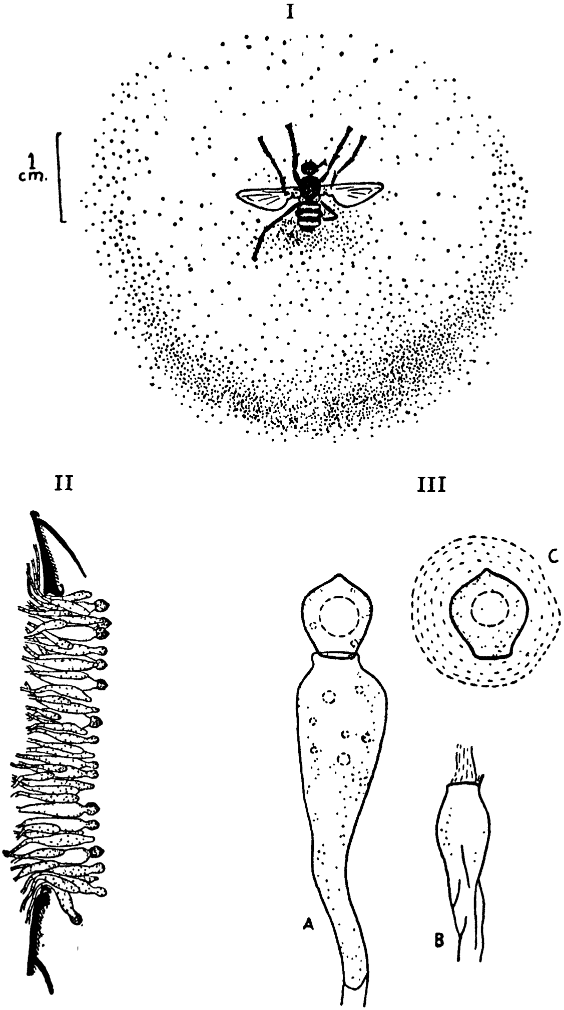

FIG. 35. *Empusa muscae.*

I, Dead fly attached to glass by its mouth-parts and surrounded by a halo of discharged conidia. Note the three white bands of conidiophores on its abdomen. II, Part of a section through the abdomen of a dead fly, showing the conidiophores projecting through the integument of the insect. × 100. III, *A*, single mature conidiophore; *B*, conidiophore after discharge; *C*, discharged conidium surrounded by a drop of conidiophore sap. × 400.

abdomen so that it appears to have several white transverse stripes. A conidium is borne terminally on each conidiophore which is simple and somewhat inflated. The conidiophore bursts, just as in *Pilobolus*, shooting the conidium to a distance of 1–1·5 cm. The result of the bursting of thousands of conidiophores is that the dead fly becomes surrounded by discharged spores forming a white halo 4–5 cm. in diameter.

Discharge due to rounding-off of turgid cells

The shape of a turgid cell is often modified by adhesion to other cells. Thus each polyhedral cell of the cortical parenchyma of a stem or root tends to become spherical, but is prevented from so doing by the presence of its neighbours. The individual cells of the tissue are under conditions of strain. In Fungi there are a number of scattered examples in which sudden change of shape by turgid cells in a state of strain results in violent spore discharge.

Discharge in Entomophthorales

Entomophthorales is a small order, mainly of fungi parasitic on insects, and one of its most constant features is that the terminal conidium is shot from its conidiophore. Two examples (*Basidiobolus* and *Empusa*) where discharge is due to the bursting of the conidiophore have already been considered, but in species of *Entomophthora* the conidia are discharged just as far, but by a mechanism involving the sudden rounding-off of turgid cells.

Entomophthora coronata (= *Conidiobolus villosus*) which grows very readily as a saprophyte on ordinary laboratory media, but in addition parasitizes termites and aphids, is a useful species for seeing this type of discharge. The terminal conidium is separated from its simple conidiophore by a cross-wall which bulges into the spore as a hemispherical columella (Fig. 36). The cross-wall is a double structure, one layer belonging to the spore-wall, the other to the apex of the conidiophore. Suddenly the incurved part of the spore-wall bulges outwards so that the spore springs off from the conidiophore to a distance of 0·5–4·0 cm. The walls of the spore and of the conidiophore, except where they are in contact in the columella zone, are two-ply structures, the outer layer of the conidiophore wall being continuous with the outer layer of the spore-wall. As a preliminary to discharge, rupture of this outer layer occurs along the circular line where the spore

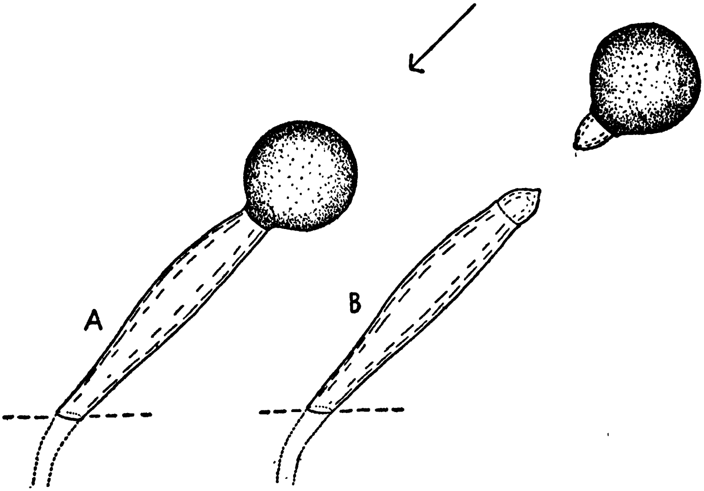

FIG. 36. *Entomophthora coronata.*

A, conidiophore just before spore discharge, with the columella seen through the semi-transparent wall of the conidium. Surface of the agar on which the fungus is growing indicated by interrupted line. Wall of conidiophore below agar surface dotted. *B*, same at moment of discharge. Arrow indicates direction of light. × 500.

joins its conidiophore. Probably as soon as this rupture occurs the spore is shot away.*

In *Entomophthora sphaerosperma*,† a parasite of the firefly, discharge occurs just as in *E. coronata*.

Downy mildews

Weston‡ has reported spore discharge very closely resembling the *Entomophthora* type in *Sclerospora philippinensis*, one of the downy mildews (Peronosporales) which attacks maize in the Philippines. The mycelium of the fungus is in the intercellular spaces of the leaf, and the branched conidiophores project in tufts through the stomates, being produced only during the night when a film of dew is deposited on the surface of the leaf. Although the lower parts of the branched conidiophores are immersed in dew, the tips bearing the spores project into the air. From each tip a single conidium is formed, and the small surface of contact between the two is flat (Fig. 37). Both the spore and the conidiophore are turgid cells, so there is a tendency for each to round off in this flattened region—a tendency counteracted by the adhesion of the two walls to one another. It seems that the rounding-off of the spore and the conidiophore tip occurs suddenly and in consequence the spore is shot away to a distance of a millimetre or two. All the spores of a single conidiophore are, apparently, discharged simultaneously. It is only in *Sclerospora* that violent discharge of this type has been reported, but another type of mechanism—a hygroscopic mechanism—has been described in other genera of downy mildews.

Aecidiospore liberation in Rusts

In rust-fungi at the base of each aecidium or 'cluster-cup' is a closely set palisade of basal cells each cutting off

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* Martin (1925).

† Sawyer (1931).

‡ Weston (1923).

an ever-growing chain of cells with aecidiospores and separating-cells alternating. The separating-cells soon break down, leaving the spores stuck together by blobs of sticky material resulting from their disintegration. In the aecidium the spores are tightly packed and each assumes a polyhedral form (Fig. 38) due to the pressure of its neighbours. Under damp conditions the spores absorb water, and with increasing turgor each tends more strongly towards the spherical form. Spores in the outermost layer of

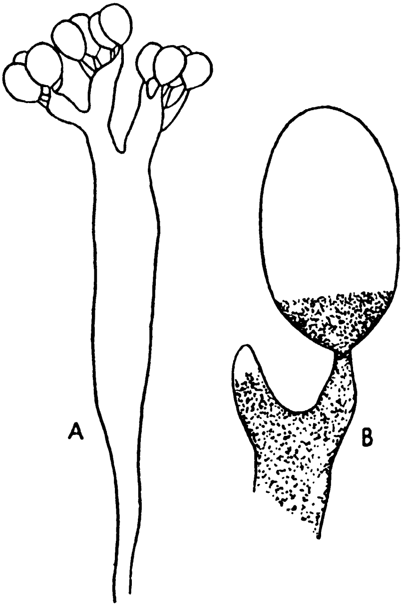

FIG. 37. *Sclerospora philippinensis.*

A, conidiophore bearing eleven conidia. *B*, part of conidiophore more highly magnified; from the left-hand tip the conidium has been discharged; on the right-hand one the conidium is still attached. *A* × 470; *B* × 1,250. After Weston (1923).

the aecidiospore mass round off suddenly and in doing so spring out either singly or in small groups to a distance of 0·5–1·0 cm.* These spores are followed by more and so the aecidium tends to empty, but the supply is renewed from the base.

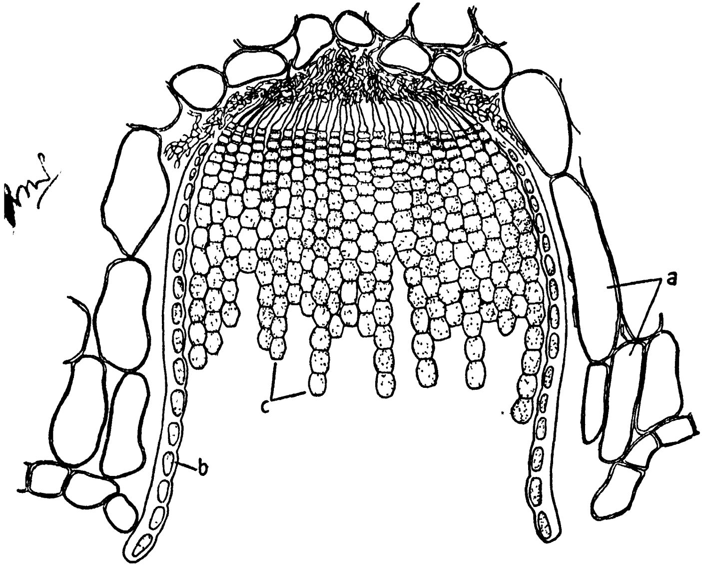

FIG. 38. *Puccinia graminis*. Aecidium in vertical as seen in transverse section of rusted barberry leaf.

a, host tissue; *b*, pseudoperidium; *c*, chains of aecidiospores. × 400.

Sphaerobolus

In *Sphaerobolus stellatus*, classified in Gasteromycetes, the sudden release of a tissue tension, which does not involve the bursting of any cells, leads to the discharge of a macroscopic spore-mass to a considerable distance.

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* Zalewski (1883); Dodge (1924); Buller (1924).

It seems quite clear that Gasteromycetes is a polyphyletic group of fungi, derived, probably, from hymenomycete ancestors. However, if these fungi ever possessed the hymenomycete equipment of spore liberation, it has now been lost and other methods have been developed. The Gasteromycetes can fairly be regarded as an assorted collection of experiments in dispersal. Thus the spores of the stink-horns and their allies (Phallaceae) are spread by insects, the puff-balls and earth-stars (Lycoperdaceae) have evolved dry-spore wind-dispersal mechanisms, the subterranean forms (Hymenogastraceae) apparently rely on rodents, the bird's-nest fungi (*Crucibulum* and *Cyathus*) have a highly specialized rain-splash mechanism, and in *Sphaerobolus* a unique type of violent discharge has been developed.

Sphaerobolus stellatus is a common saprophyte on old, rotten wood, and the tiny fruit-bodies, each about 2 mm. in diameter, are commonly to be seen in autumn, usually crowded together in large numbers (Plate VI). The unopened fruit-body is spherical and anchored to its substratum by fine hyphae. In section it is found to consist of a central spore-containing region (gleba) surrounded by a wall (peridium) differentiated into six histologically distinct layers. When the fruit-body is mature, the peridium splits along a number of lines radiating from the apex. In this way from four to eight little teeth of peridial tissue are delimited which bend outwards, exposing the spherical gleba. At the same time the peridium becomes separated into two little cups, fitting one inside the other, each with a toothed margin and attached together only at the points of the teeth (Fig. 39). The outer cup is composed of the three outer layers of the peridium, the inner of two of the three remaining layers. The sixth layer, which was in immediate contact with the gleba, has at this stage broken down to produce a fluid (lubricating fluid), so that the spherical glebal mass fits loosely in the inner cup, just submerged by this fluid. Forming the inner wall of the inner cup is a palisade tissue of relatively large cells which in the unopened fruit-body are radially arranged, whilst the outer wall is formed by fine interwoven hyphae mostly following a tangential course. The cells of the palisade layer in contact with the lubricating fluid absorb water, so that the area of the inner surface of the cup tends to increase, but where they are in contact with the layer of interwoven hyphae such increase is impeded. In this way strains are set up which are suddenly and violently released by the inner cup turning inside out, thereby catapulting the gleba to a distance of up to 550 cm. (Fig. 40).

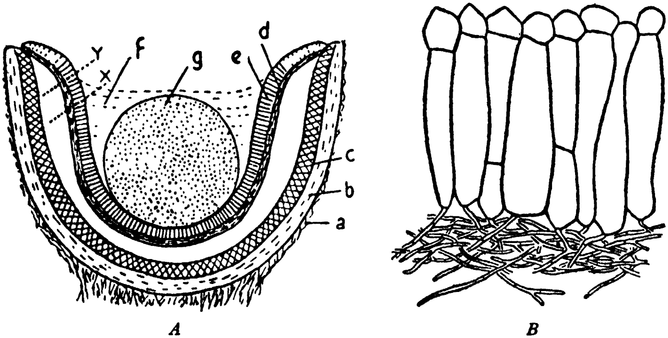

FIG. 39. *Sphaerobolus stellatus*. Diagram illustrating discharge of gleba.

A, immediately before discharge. Outer cup consists of: *a*, layer of loose hyphae; *b*, gelatinous layer; *c*, pseudoparenchymatous layer. Inner cup consists of: *d*, layer of tangential hyphae, and *e*, palisade layer. The gleba (*g*) lies loosely in the lubricating fluid (*f*). *B*, part of inner cup (between lines *X* and *Y* in *A*) highly magnified.

Ballistospores

The name 'ballistospore' has been given to the type of spore which is perched asymmetrically on a fine sterigma and in which the secretion of a drop of liquid by a small projection (hilum) of the spore immediately precedes spore discharge.*

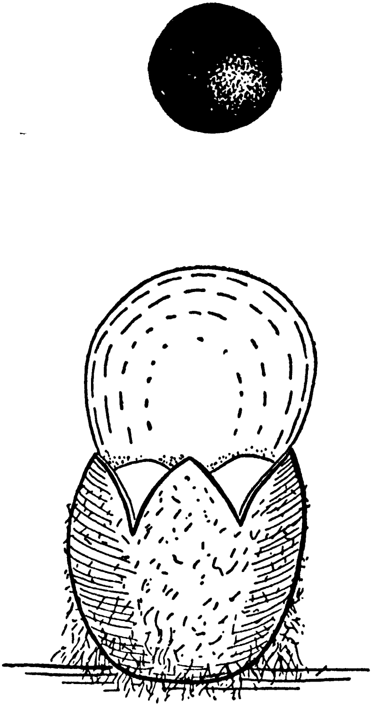

FIG. 40. *Sphaerobolus stellatus*. Fruit-body, growing on wood, at the moment of discharge. The inner cup has turned inside out, exposing its wet, shining surface. × 16.

The basidiospores of Hymenomycetes and gelatinous Basidiomycetes are ballistospores, and so also are the

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* Derx (1948).

sporidia (basidiospores) of rusts (Uredinales) and the conidia of certain smuts (e.g. *Tilletia caries* and *Entyloma* spp.)* and of shadow yeasts (Sporobolomycetaceae) (Fig. 41).†

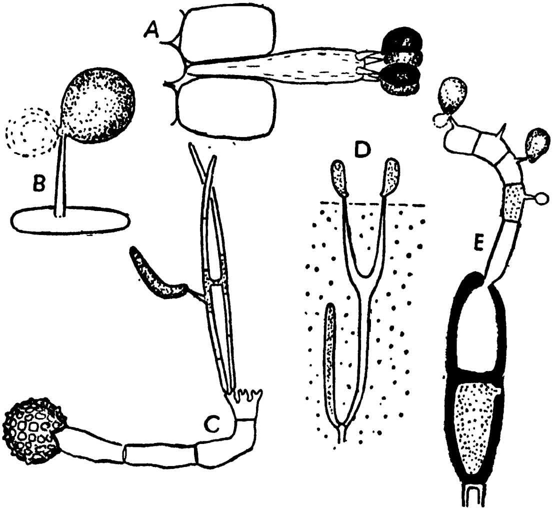

FIG. 41. Ballistospores.

A, Basidium of *Coprinus micaceus*, × 680; *B*, *Bullera alba* (shadow yeast) with ballistospore abou to be discharged, × 1,700; *C*, ballistospore (secondary conidium) of *Tilletia caries*, × 440; *D*, basidium of *Dacryomyces deliquescens*, × 360; *E*, teleutospore of *Puccinia malvacearum* with upper cell germinated to give promycelium (basidium) bearing ballistospores, × 490; *C* and *D* after Buller.

The basidiospore of *Puccinia malvacearum* (hollyhock rust) may be considered as a typical ballistospore (Fig. 42). In this rust, when the two-celled teleutospore is placed in a damp atmosphere, a short hypha is produced from each cell. This curved hypha is the young basidium. It becomes divided into four cells from each of which, on the convex side of the curve, a short sterigma grows out and

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* Hanna (1938).

† Buller (1933).

swells at its tip to form a spore. From its first appearance as a minute enlargement of the tip of the sterigma it grows to full size in about forty minutes, and ten minutes later is shot away. Near its attachment to the sterigma the spore has a small blunt, beak-like projection—the hilum. From this, just before discharge, a drop of fluid appears, grows steadily to a certain definite size, and then at once

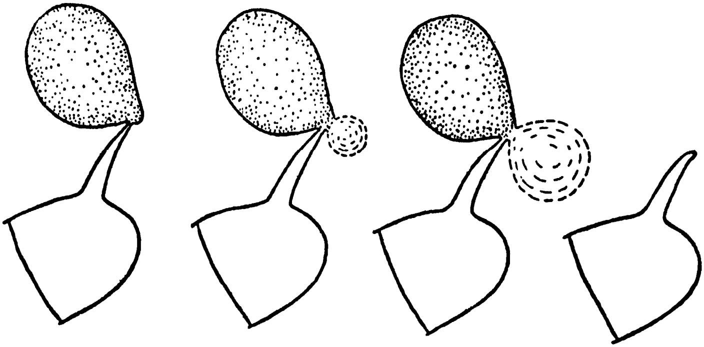

FIG. 42. *Puccinia malvacearum*. Stages in spore discharge. × 2,000.

the spore is shot away, carrying the drop with it. No liquid is to be seen at the end of the vacated sterigma, which exhibits no observable shrinkage.

Ballistospores show little range in size and shape as compared with ascospores, and the distance of discharge is small also and varies within narrow limits (0·1–1·0 mm.).

The mechanism responsible for the violent discharge of ballistospores still remains in doubt, but there are three current theories worthy of mention. One theory* is that discharge is due to the bursting of a turgid cell, as in *Pilobolus*. Now the unicellular basidium of Hymenomycetes bears four ballistospores which are discharged

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* Buller (1922).

in succession, with a short interval between the liberation of sister spores. If each spore is discharged by the bursting of its sterigma, it is difficult to see how, after one sterigma has burst at its apex, projecting its spore, the end becomes sealed to allow maintenance of turgor in the basidium so that the next spore in succession can be shot away. Further, there is no noticeable and immediate shortening of the sterigma following discharge, nor is any fluid normally to be seen at its apex. Certainly, if the sterigma bursts it would be expected that escape of basidial content, in the form of a small drop, would occur before the sterigma could have time to become sealed again. A second theory* is that the surface energy of the drop excreted at the hilum is used in some way to effect discharge, but there is no definite evidence to support this view and its only merit is that it brings the exuded drop of the ballistospore into the picture. A third theory is that discharge may be of the type already recorded for *Entomophthora* and *Sclerospora*. In recent years this old theory has been advocated again by Prince,† who made a careful study of basidiospore liberation in *Gymnosporangium nidus-avis*. The basidiospore of this rust is a little unusual because the prominent beak on the spore is not the hilum, but is where the spore is actually attached to the sterigma. The hilum itself cannot be detected in the liberated spore, and in the attached one can be located only when drop-exudation occurs. Prince found that where the mature spore joins the sterigma there is a clearly defined cross-wall which is flat. It is interesting to note that Buller, in his observations on the development and liberation of basidiospores, was unable to satisfy himself that such a cross-wall existed. However, *Gymnosporangium nidus-avis* appears to be exceptionally suitable material for seeing the nature of the

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* Ingold (1939).

† Prince (1943).

junction between the spore and its sterigma, and there can be no doubt of the correctness of Prince's observation. Further, Prince found that immediately following discharge both the end of the sterigma and the beak of the spore showed convex surfaces, not flat ones. He suggests that it is sudden rounding-off at the flat surface of contact that is responsible for violent discharge, just as in *Sclerospora*. If Prince's picture (Fig. 43) of spore liberation in *Gymnosporangium* can be applied generally to ballistospores, there still remains the mystery of the asymmetrical perching of the spore on its sterigma and the significance of drop excretion. Prince has made the interesting observation that if a ripe basidium is mounted in water, discharge preceded by drop excretion may still be seen. Presumably there is a membrane around the drop which prevents its mixing with the water.

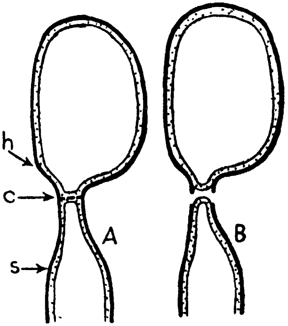

FIG. 43. *Gymnosporangium nidus-avis*. Diagram of basidiospore.
A, just before discharge; *B*, at moment o discharge. *h*, hilum (exuded drop not shown); *c*, cross-wall separating spore from sterigma (*s*). After Prince (1943).

Fruit-bodies of Hymenomycetes in relation to ballistospore discharge

In Hymenomycetes the fruit-body, usually large and conspicuous, bears extensive exposed hymenia in which millions of basidia occur interspersed with sterile cells. Each basidium is a single turgid cell which, like the ascus, is a special kind of sporangium, but instead of the spores being produced internally they are formed externally and are characteristic ballistospores. Usually there are four spores grouped around the apex of the basidium. Each is borne asymmetrically on a very fine sterigma with the hilum pointing inwards.

It has been seen that the chief factors governing the form of the apothecium in Discomycetes are that the spores are usually squirted to a distance of several centimetres, that the asci are positively phototropic, and that the hymenium is not damaged by water. In the same way the architecture of the hymenomycete fruit-body seems to have been governed by certain simple facts, namely that the spores are discharged to a distance of less than half a millimetre, that the hymenial surfaces can be orientated by geotropic movements, and that the hymenium is spoilt, at least temporarily, by water. Since the distance of spore discharge is so small the upward-facing hymenium is inefficient as the sticky spores would tend to fall back almost immediately on to the parent surface and so be wasted. Further, such an hymenium would be continually subject to injury by rain. Thus, hymenial surfaces tend to be displayed in fruit-bodies either in a vertical or a downward-facing position between the horizontal and the vertical, and where the vertical position is assumed there is usually, except in the Clavariaceae, an adequate protection from rain.

The escape of spores from the agaric fruit-body

Russula ochroleuca (Fig. 44), one of the commonest of woodland agarics, may be taken as a fairly typical example of a toadstool fruit-body. The hymenium covering the gills consists of basidia intermixed with sterile cells of two kinds: paraphyses that are difficult to distinguish from young basidia from which sterigmata have not yet sprouted, and conspicuous cystidia with pointed ends and granular contents. In the majority of toadstools cystidia are absent and the hymenium is composed solely of basidia and paraphyses. In any small area of the hymenium basidia are to be seen at all stages of development. Those that have discharged all four spores are still turgid cells

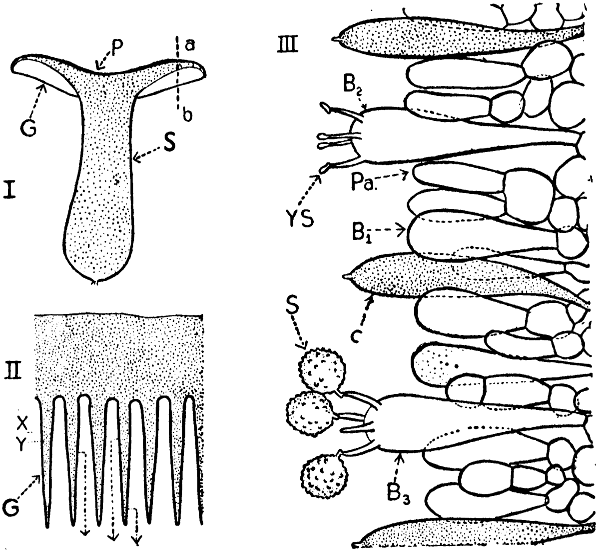

FIG. 44. *Russula ochroleuca.*

I. *L.S.*, fruit-body; *S*, stipe; *P*, pileus; *G*, gill. II, part of vertical section along line *a–b* in I at right angles to the paper; *G*, gill, with hymenium shown by thick black line. III, hymenium between *X* and *Y* in II; B_1, B_2, B_3, basidia of increasing maturity; *Pa*, paraphys; *C*, cystidium; *S*, basidiospore; *YS*, young spore. I × ½; II, × 2·5; III, × 610.

and look very much like young basidia that have just formed their sterigmata but in which spore-formation has not yet begun. However, the exhausted basidia are clearly differentiated from young ones by having little remaining protoplasm, and they soon collapse and disappear.

The pileus in *Russula ochroleuca* is supported on a central stalk (stipe) which, as in most toadstools, is a fairly rigid structure so that the sporophore shows no tendency to sway in the wind. The importance of the stipe depends partly on its rigidity and partly on the fact that it provides a space between the pileus and the ground, thus affording an opportunity for the falling spores to be swept away by air currents.

In connexion with the function of the stipe it is interesting to note how size and form seem to be related in the agaric fruit-body. The weight of the cap, roughly proportional to its volume, acts vertically on the stipe and the strain is distributed over the area of the cross-section. If it is assumed that organisms are economical with their tissue, it might be expected that the stipe would tend to be of a thickness just sufficient to support the pileus with the rigidity necessary for the proper functioning of the sporophore. Now in solid figures, that vary in size but not in form, the volume varies as the cube of the linear dimensions, but two-dimensional features vary as the square. Thus the volume and, therefore, the weight of the pileus varies as the cube of its diameter, but the cross-section of the stipe varies as the square of its width. On these considerations it would be expected that the agaric sporophore would not remain constant in form with change of size, but that, as compared with a median type, the smaller fruit-bodies would tend to have relatively slender stipes and the larger ones relatively thick ones. Again, the height of an agaric is mainly due to the length of the stipe, which provides a space between the under side of the cap and the ground, so that spores in their downward course have a good chance of being blown away before they reach the ground in the immediate vicinity of the fruit-body. With the development of larger and smaller types of agarics it might be expected that the general form would tend to be preserved. However, in the larger types the interval between cap and substratum would tend to become greater than necessary and it might be expected that mutants having shorter stalks, and thereby economizing tissue, would tend to survive in the struggle for existence. On the other hand, in the smaller types, if the form remained unaltered, the interval between the pileus and the ground might be reduced too far for efficient dispersal and mutant types with longer stalks would tend to be selected. Thus we might expect that the larger sporophores would tend to be relatively short and the smaller ones relatively tall.

Both these expectations are fulfilled, and it is found that in fact small agarics tend to be relatively tall and have relatively thin stalks and large agarics tend to be relatively short and have relatively thick stalks as compared with those of medium size.*

In a fruit-body such as that of *Russula ochroleuca* the hymenial surfaces are brought into a vertical position by growth movements in response to external stimuli. In some agarics (e.g. *Coprinus cinereus*) the stipe in the young fruit-body is positively phototropic, but in others (e.g. *Psalliota campestris*) there is no phototropic response. However, in all species the stipe finally reacts strongly to gravity by growing vertically upwards, thus giving a rough vertical orientation to the gills that hang down on the underside of the cap. But (except in *Coprinus* spp.) in addition each individual gill is positively geotropic, so that if a fruit-body is displaced in such a way that the gills depart slightly from the vertical, each one undergoes growth adjustments until it is once more in the vertical plane.

The adjustment of fruit-bodies in response to gravity can be clearly seen in toadstools that happen to be growing

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* Ingold (1946 *a*).

on steep slopes (Fig. 45). The region of geotropic curvature of the stipe is just below the pileus. The fine adjustment by positive geotropism of the hymenium-bearing structures is not limited to the gills of agarics, but is also found in the tubes of *Boletus* spp. and in the spines of *Hydnum* spp.

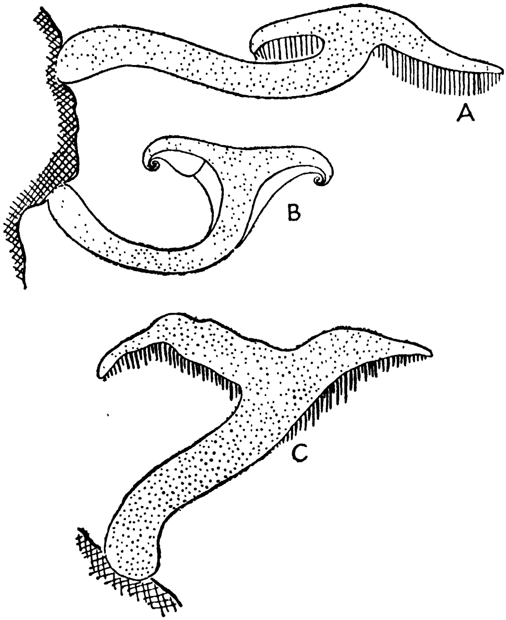

FIG. 45. Sporophores of toadstools growing on highly inclined surfaces. Negative geotropism of stipe brings pileus approximately into horizontal position and the hymenial surfaces are subject to a fine adjustment due to positive geotropism of the gills (e.g. *B*, *Paxillus involutus*), tubes (e.g. *A*, *Boletus chrysenteron*), or spines (e.g. *C*, *Hydnum repandum*).

Although in fleshy toadstools gravity plays such an important part in the final adjustment of the fruit-body, it has no *formative* effect. Thus if a tube-slant of nutrient agar is inoculated with *Collybia velutipes*, a species that fruits exceptionally well in culture, and if this tube is rotated continuously for several weeks about a horizontal axis on a klinostat, thus eliminating any unilateral action of gravity, normal fruit-bodies are produced.*

In toadstools Buller has shown that the spores are shot from the horizontal basidia to a distance of 0·01–0·02 cm. into the spaces between the gills. They then fall and, on emerging into the open air below the pileus, can readily be dispersed by quite gentle winds or even convection currents. If the sticky spores fall on to the hymenium surface they remain stuck there. For this reason the vertical position of the gills is essential if wastage of this nature is to be avoided. In addition, for successful spore liberation the gills must be farther apart than the distance to which the spores are shot and there is, in fact, usually a considerable margin of safety.

Spore liberation in Coprinus

The organization of the fruit-body in the genus *Coprinus* (ink-cap fungi) is especially interesting and has been thoroughly investigated by Buller.† Probably the *Coprinus* apparatus represents the most advanced type amongst toadstools. *Coprinus atramentarius* may be taken as a beautiful example. Most ink-caps are more or less coprophilous, but *C. atramentarius*, a relatively large and very common species, grows on buried wood and is often to be seen at the base of old gate-posts. The structure of the sporophore is illustrated in Fig. 46. It is clear that for the size of the fruit-body the amount of pileus tissue is very small. Further, the gills are remarkably thin (0·1–0·15 mm.), very numerous, and close together, being only 0·15–0·2 mm. apart. They are, however, prevented from

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* Plunkett (unpublished).

† Buller (1924).

touching by large cylindrical cystidia (0·12–0·17 × 0·02–0·03 mm.) which occur in the hymenium and which stretch across to the opposite gill (Fig. 47). In most agarics basidia on any small area of the hymenium are at very different stages of development, but in the genus *Coprinus*, in a small area such as appears in the high-power field of the microscope when the gill is seen in surface view, all the basidia are roughly at the same stage (Fig. 48 and Plate VII). A wave of development passes from the free margin of each gill upwards towards the pileus tissue. Young basidiospores are colourless, but change as they ripen through pink to dark brown or almost black. It is the spores that give the colour to the gill. So in a fruit-body

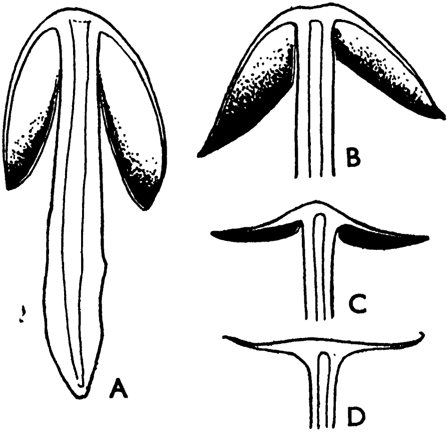


FIG. 46. *Coprinus atramentarius*. Sporophore in vertical section.

A, at the beginning of spore liberation: the free margin of the gill has shed its spores and is colourless; behind this the gill is black with ripe spores grading off through pink (dotted region) to white. In *B* the cap has expanded and a small part of each gill has been removed by autodigestion. In *C* most of the gill tissue has been autodigested, and in *D* the process is complete. After Buller (1924). × ½.

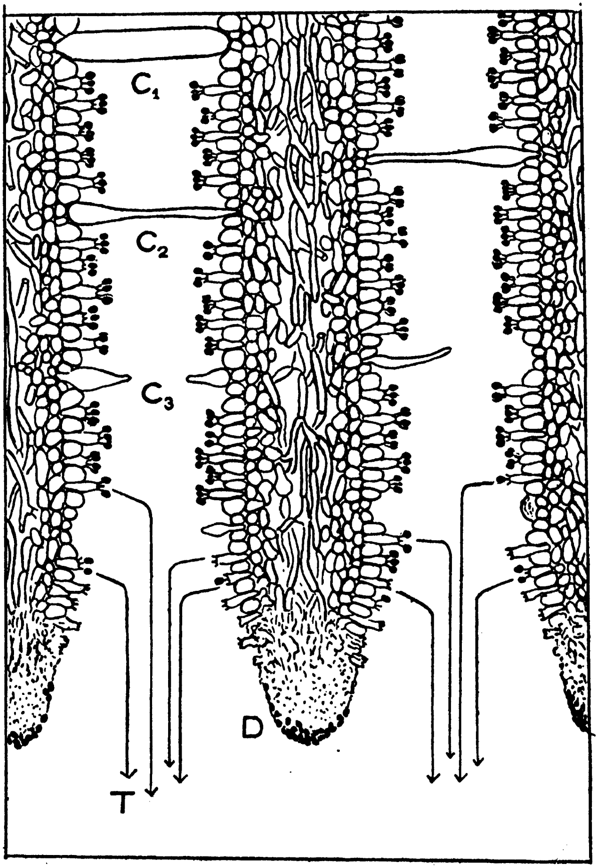


FIG. 47. *Coprinus atramentarius*. Tangential vertical section of cap, showing gills in sectional view.

C_1, unaltered cystidium; *C_2* and *C_3*, stages in autodigestion of cystidia; *D*, autodigesting edge of gill with a few spores trapped in the resulting slime. *T*, trajectories of spores being discharged from the basidia. Note the short distance of spore-fall between opposing gill surfaces. × 136. After Buller (1924).

from which spores are escaping each gill is blackish towards its free margin and grades through pink to white as the pileus tissue is approached (Fig. 46). As the spores are shot away a very narrow zone near the gill margin

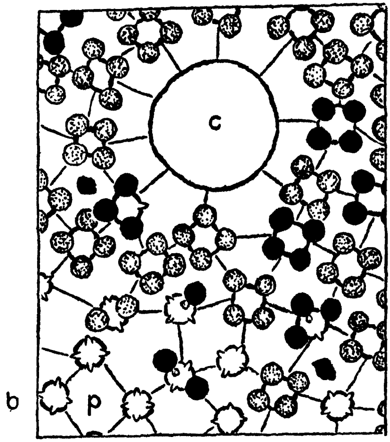


FIG. 48. *Coprinus atramentarius*. Small part of the ripe region of the gill in surface view. The base of the picture is near the free edge of the gill and near the bottom are basidia from which all the spores have been discharged. All the spores are black, but those on the shorter basidia have been stippled to distinguish them from those on the longer (shown black). *b*, basidium which has discharged its spores; *p*, paraphysis; *c*, cystidium. × 440. After Buller (1924).

becomes white due to the loss of its spores, and this spore-depleted area rapidly undergoes a process of autodigestion resulting in its liquefaction. The fluid formed in this way turns black and under highly humid conditions may flow down the inclined margins of the gills and accumulate as inky drops at the edge of the pileus. However, if conditions are drier the liquid produced by autodigestion evaporates and no inky drops are formed. Most of the spores shot from the basidia escape, but a certain number drift into the inky liquid and get stuck. In *Coprinus atramentarius* the stipe is negatively geotropic and this reaction brings the gills roughly into a vertical plane. But the gills themselves are not geotropic. However, their failure to respond to gravity does not militate against the efficiency of spore liberation, since, due to the removal of exhausted hymenium by autodigestion, the spores have only a fraction of a millimetre to fall between gill surfaces before emerging into the free air below the cap.

The behaviour of the cystidia is especially interesting. These undergo autodigestion somewhat before the rest of the gill and disappear just before spore discharge in their vicinity begins (Fig. 47). In this way they offer no obstacle to the escape of the falling spores. In *C. atramentarius* the basidia are dimorphic—there are longer and shorter ones. This arrangement allows closer packing in the hymenium than would otherwise be possible. Further, the longer basidia mature and discharge their spores slightly earlier than the shorter ones, so that the ballistospores of the shorter basidia can be discharged without colliding with spores on the longer basidia (Fig. 47).

Spore liberation from an annual bracket polypore

Polyporus betulinus, a birch parasite which, having killed the host, produces its fruit-bodies on the trunks and limbs of the dead tree, may be taken as a familiar example of a bracket polypore. Gravity has a profound formative influence on the sporophore. The young fruit-body first appears erumpent as a small, undifferentiated spherical knob 2–3 cm. across. If this is on the main vertical trunk, it then grows out horizontally (diageotropism) to form a firm, more or less semicircular structure, with a radius of 15–20 cm. and about 3 cm. thick, attached laterally to the trunk (Fig. 49 A). If, however, the original spherical primordium is on the under side of an approximately horizontal branch, the fruit-body develops a roughly circular form with a central attachment to the tree

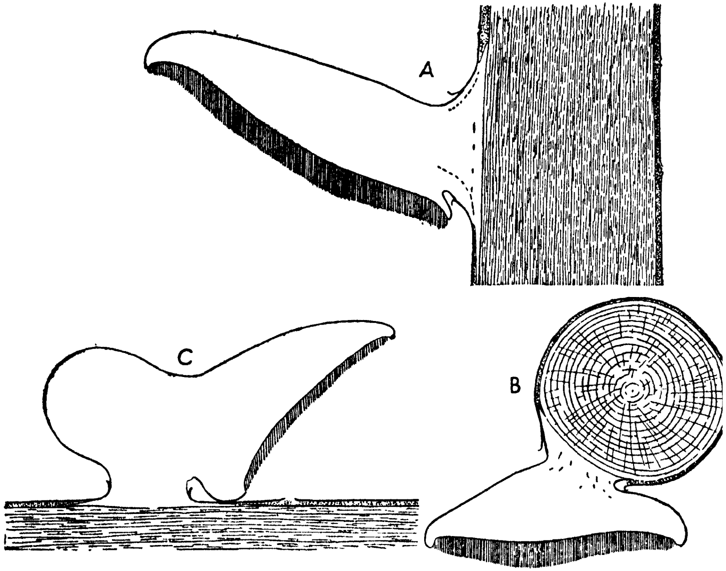


FIG. 49. *Polyporus betulinus.*

A, L.S. through trunk of small birch tree, showing sporophore; B, T.S. horizontal branch of birch, showing sporophore on under side; C, sporophore, on upper side of felled birch trunk, developed from primordium which arose when the trunk was erect. × ⅜.

(Fig. 49 B). Fruit-bodies do not normally arise on the upper side of a branch, but if a dead tree bearing primordia is felled, those on the recumbent trunk may continue their development. A primordium thus exposed on the upper surface of a fallen trunk grows out on one side only, more or less at right angles to the pull of gravity (Fig. 49 C).

It is, apparently, gravity also that determines the formation of the hymenial pores on the under surface of the fruit-body. These pores are at first very shallow, but throughout the life of the sporophore (September to April) they grow by means of an active zone around the mouth of each pore, so that gradually they become longer. The direction of growth is conditioned by gravity so that the tubes produced are orientated precisely in the vertical direction. This gradual geotropic growth of the tubes is in contrast to the state of affairs in a toadstool, where gravity is not concerned in the development of the hymenial surfaces but only in their final orientation. In bracket polypores geotropic growth achieves the desirable result of vertical hymenial surfaces, but if these, once formed, are slightly displaced from the vertical, there is no mechanism of readjustment in the pores. This is in striking contrast to the *Boletus* type of polypore.

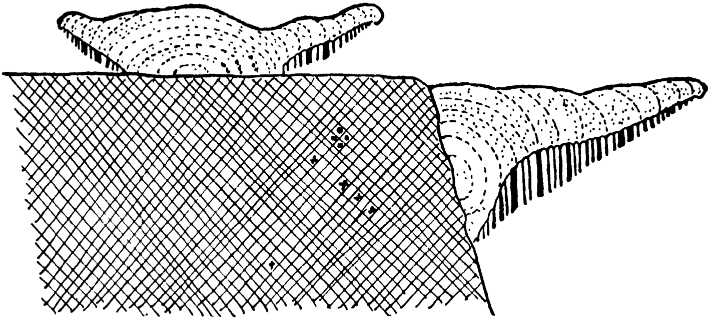


FIG. 50. *Trametes gibbosa.* Beech stump with a sporophore on its top and on its side. × ½.

In *Trametes gibbosa* (Fig. 50), so common as a saprophyte on beech stumps, the morphogenesis of the sporophore is similar to that of *Polyporus betulinus.* Here the fruit-bodies arising on the more or less vertical surface of the trunk are of the bracket form, whilst those on the transversely cut surface of the stump are radially symmetrical with a very broad central attachment. The pores are normally formed on the under surface, probably in response to gravity, but the mechanism appears not infrequently to fail, since shallow pores bearing an active hymenium are occasionally to be found on the upward-facing surfaces.

In *Polyporus betulinus* the hymenial tubes almost from their first inception are lined with active hymenium and spore discharge takes place during the whole period of several months during which the pores are elongating.

Apart from the rather striking difference in the developmental picture of the sporophore, the general story of spore liberation is the same as in agarics. The spores discharged into the tubes fall vertically and on emerging from the under side of the bracket are carried away by wind.

Perennial bracket polypores

In the genera *Fomes*, with white spores, and *Ganoderma*, with brown, certain species produce large woody brackets which are perennial. As an example the common and world-wide species *Ganoderma applanatum* may be considered. It is frequently found on the trunks of broad-leaved trees, especially beech. As in *Polyporus betulinus*, gravity has a determining formative effect on fruit-body development. Because of its extremely hard and rigid structure, and because of the broad and firm attachment to the tree trunk, the hymenial tubes formed by geotropic growth are very accurately orientated and there is little likelihood of even the slightest subsequent displacement from the vertical. Apparently correlated with this rigidity of construction the hymenial tubes are exceedingly narrow, having a diameter (0·15 mm.) probably little more than the distance to which the spores are discharged. Unfortunately there are no measurements of this distance for the ballistospores of *Ganoderma applanatum*. The distance apart of the gills in *Coprinus atramentarius* is almost the same as the diameter of the tubes in *Ganoderma applanatum*, but in the former the spores have only a fraction of a millimetre to fall between hymenial surfaces before emerging into the open air, whereas in the latter a spore may have to fall several centimetres before escaping from the tubes.

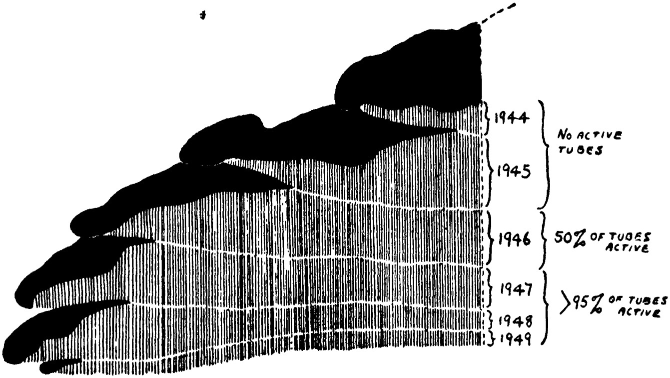
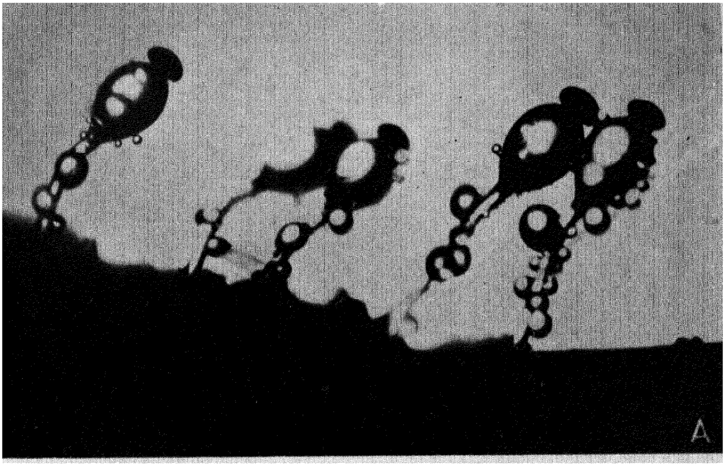


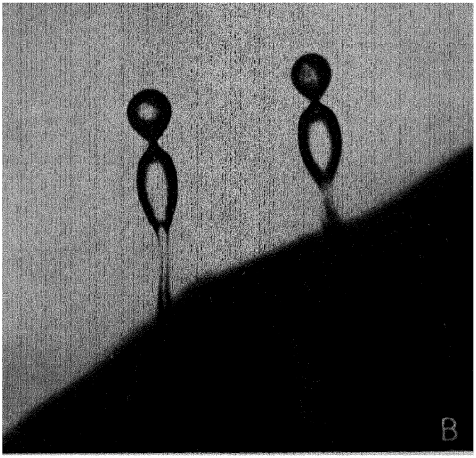
FIG. 51. *Ganoderma applanatum.* Fruit-body gathered from beech trunk in July 1949 and here seen in vertical section. A part of it, where it joins the bark of the tree, is omitted. Sterile pileus tissue shown black. Six annual layers of tubes are visible. The tubes are continuous from one layer to the next, but are shown interrupted at the end of each year's growth to distinguish the annual layers. × $\frac{2}{3}$.

In *Ganoderma applanatum*, and also in *Fomes fomentarius*, not only the fruit-bodies but also the hymenial surfaces themselves are perennial. A typical specimen of *G. applanatum* collected in July 1949 is illustrated in Fig. 51. Six annual layers of hymenium tubes are seen. In the 1949 layer active hymenium was found throughout the length of each tube with the exception of the youngest half millimetre where basidia were absent because, no doubt, of its recent formation. In the 1948 and 1947 layers more than 90 per cent. of the tubes were lined with active hymenium throughout their length and the density of basidia in the hymenium appeared just as great as in that of the current year. In the 1946 layer, however, only about 50 per cent. of the tubes had a functioning hymenium; the remainder had no basidia and many of these tubes were plugged with white mycelium. Finally, in the 1945 and 1944 layers no tubes contained basidia and most were plugged. When a single tube was followed upwards from its orifice it was found normally to be continuous and to be lined with active hymenium in the lower three or four annual sections, but to be devoid of basidia higher up.

If a sporophore is cut vertically with a saw it is impossible to distinguish the boundaries separating the annual layers of tubes. If, however, a deep incision is made in the sterile upper tissue and the fruit-body is then broken by bending, the vertical surface of tubes thus exposed usually has a step-like appearance and the annual layers of tubes can easily be seen. Some structural peculiarity associated with the cessation of growth during the winter is no doubt responsible for this tendency for one annual stratum of tubes to break away from that above and below, in spite of the fact that they are not separated by layers of sterile tissue. Although for most of the hymenial tubes sealing over does not occur before the production of the next annual layer, this does happen along a semicircular band forming the circumference of the under surface of the sporophore. The hymenial tubes thus sealed have only their one year of activity, and from the under side of the semicircular strip of sterile tissue new tubes are formed in the following growing season. Thus the greater part of each annual



A, *PILOBOLUS KLEINII*, sporangiophores on horse-dung. × 12.



B, *BASIDIOBOLUS RANARUM*, conidiophores on the excreta of frogs. × 216.

PLATE V

Photo C. E. B. Dobb

PLATE VI. *SPHAEROBOLUS STELLATUS*

Group of fruit-bodies seen under a simple lens. In some the dark spore-mass is still undischarged and lies submerged in the 'lubricating fluid' within the inner cup of the fruit-body. In others discharge has occurred and the inner cup has turned inside out and now has the appearance of a pearl.

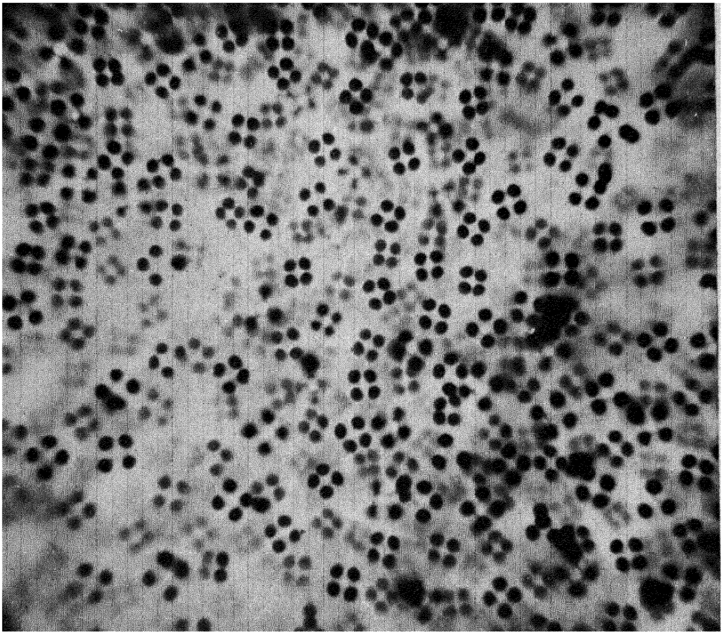


Plate VII. *COPRINUS MICACEUS*

Portion of living gill in surface view, showing spores in groups of four. × 320.

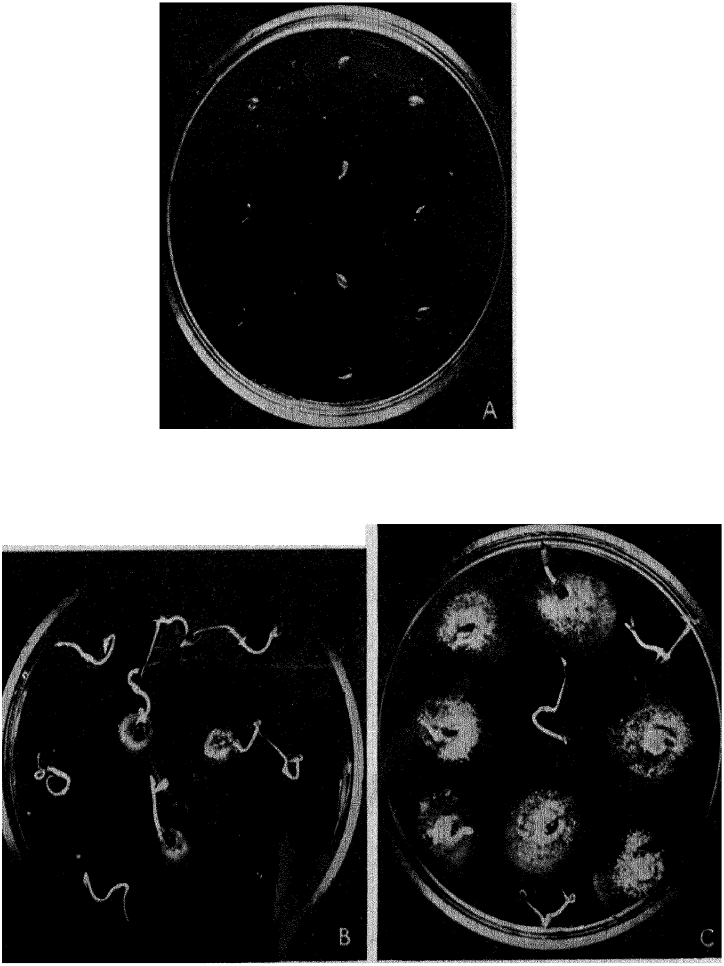


PLATE VIII

Ulster method of testing for seed-borne fungi. A, petri dish containing nutrient agar and with ten flax seeds on the surface of the medium. The dish is in readiness for carrying out a test. B, a petri dish as in A after incubation for several days. Most of the seeds have germinated and three are surrounded by colonies of *Polyspora lini*. C, similar to B, but in this dish seven of the seeds have given rise to colonies of *Colletotrichum linicola*.

(After Muskett and Colhoun (1947)).

stratum of hymenial tubes is derived from the continued growth of tubes of the previous year, but a small part consists of new tubes.

The account of the organization of the sporophore given above agrees with the observations of Faull on *Fomes fomentarius* but is at variance with Buller's account* of *Ganoderma applanatum*. He figured a sporophore in which each annual layer of tubes was completely sealed off by sterile tissue before the production of the next, so that the tubes could function only for a single season. This would seem to be what happens in a variety of *Ganoderma applanatum* sometimes separated as a distinct species, *G. vegetus*. It also is a regular feature of *Fomes ulmarius*, a common perennial bracket polypore on elm trunks.

Certain types of sporophore have been considered illustrating the principles involved in the architecture of large structures concerned with the production and liberation of ballistospores, but in addition there are other types. Thus, in *Clavaria* and related genera the fruit-body consists either of a simple club (e.g. *Clavaria pistillaris* and *C. inaequalis*) or of a branched system (e.g. *C. cinerea*) with the branches orientated vertically by negative geotropism and with the hymenium covering the branches except towards the base of the sporophore; in *Hydnum* (e.g. *H. repandum*) the general form is that of a toadstool, but the hymenium covers positively geotropic spines on the under side of the cap; and in *Stereum* and other members of Thelephoraceae the hymenium is more or less smooth, but in the development of the sporophore gravity determines the position of the hymenium so that it is vertical, horizontal and downward-facing, or at some intermediate position, but it does not face upwards. Although in some gelatinous Basidiomycetes (e.g. *Auricularia mesenterica*, *Hirneola auricula-judae*, and

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* Buller (1922).

Tremelledon) the position of the hymenium is apparently determined during development by gravity as in *Stereum*, in others (e.g. *Tremella mesenterica* and *Dacryomyces deliquescens*) the spore-producing layer may face in any direction and gravity appears to have nothing to do with its development. Critical experimental work on morphogenesis in the larger fungi is much to be desired.

External conditions and the discharge of basidiospores

Information concerning the effect of external conditions on spore discharge in Hymenomycetes is not extensive and there are few quantitative data. The main external factors that might be expected to be important are temperature, water supply, and light.

Temperature. Buller* has shown that spore discharge in *Lenzites betulina* can continue over a range of temperature of 0°–29° C., but at the extremes of this range discharge is clearly much less than at intermediate temperatures. Again, it has been shown† that chilling an active fruit-body of *Fomes fomentarius* leads to cessation of spore discharge for some days even after a return to normal temperatures.

Humidity and water-supply. The interpretation of experiments on the effect of humidity on fungi is difficult because, whatever may be the level of general humidity maintained in an experimental chamber, the actual humidity of the air in immediate contact with the surface of damp fungal tissue is likely to be close to saturation-point. So long as the water content of the hymenial tissue is kept up, spore discharge can occur irrespective of the general humidity of the surrounding air. However, dry air leads to rapid evaporation from the spore-producing surface and, unless there are available reserves of water to replenish the hymenium, loss of turgor in the basidia soon leads to a

* Buller (1909).

† Buchwald (1938).

cessation of spore discharge. The great majority of the large fleshy fungi are mesophytes that can function only under damp conditions. They rapidly lose water and cease to liberate spores in dry air and have practically no power of recovery when free water is again available. These fungi tend to be produced at periods in the year when the air and soil are relatively moist and when there is a freedom from hard frosts. In their ecological studies on the occurrence of grassland agarics Wilkins and Patrick* have demonstrated two maxima of fruit-body production—a minor one in May and the major one in autumn. The gelatinous and leathery lignicolous basidiomycetes, on the other hand, are in the main drought-enduring xerophytes. Under dry conditions water is lost and spore discharge ceases, but with the return of wet conditions water is rapidly absorbed and spore discharge soon starts again. In this connexion *Schizophyllum commune*, a small bracket agaric commonly seen on fallen beech trunks, has been carefully studied and it has been shown in tests, started by Buller and now carried on by Bisby, that fruit-bodies can remain stored in a dry state for twenty-five years and then, a few hours after wetting, freely liberate viable spores.† However, in nature, in *Schizophyllum* and in most other leathery bracket fungi, a fruit-body lasts for only a single season. The drought-enduring type of xerophytism of these lignicolous Basidiomycetes is comparable with the xerophytism of the Pyrenomycetes of wood and bark.

The water-relations of spore liberation in the perennial polypores call for special mention. In *Ganoderma applanatum* spore discharge is continuous day and night from May to October,‡ and even after long periods of summer drought of six to eight weeks' duration, ferruginous clouds of spores

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* Wilkins and Patrick (1940).

† Bisby (1945).

‡ White (1919).

can be seen escaping from the under side of a sporophore. However, when a sporophore is detached from its tree trunk, brought into a dry laboratory, and carefully arranged so that its hymenial tubes are vertical, spore discharge continues only for a day or two. Water rapidly evaporates both from the under side and from the firm crust of the upper surface, and no doubt this leads to the turgor of the hymenial surfaces falling below the critical level for spore discharge. Thus the continuance of discharge from the fungus on the tree cannot be due to water reserve in the fruit-body, but is probably due to maintenance of turgor by the translocation of water from the tree trunk making good the considerable loss of water in transpiration by the sporophore. The water reserve in the wood is not only the water present as such in the tree trunk, but also the water combined in the carbohydrates of the woody tissues which are broken down by the fungal mycelium, with the incidental production of water. It has been calculated that the decay by a wood-destroying fungus of the cellulose in 1 cubic metre of wood might yield 139 litres of water. Buchwald* records a striking instance which shows how little these perennial polyphores depend on atmospheric humidity and rain. A large specimen of *Fomes fomentarius* was found in January on poplar, and, the host being unusual, a section of the trunk bearing the sporophore was cut from the tree and brought into a Copenhagen museum, where it was exhibited uncovered on a table (Fig. 52). The following spring the fruit-body began to liberate spores in dense white clouds. Spore discharge continued for many weeks. The present writer has brought a healthy fruit-body of *Fomes fomentarius*, detached from its substratum, into the laboratory in May, but spore liberation, though at first very vigorous, continued only for two

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* Buchwald (1938).

days, so that evidently there is insufficient water reserve in the sporophore to maintain discharge. Here again it seems that the reserve of water in the wood is being used by the fungus and translocated into the fruit-body, thus maintaining the turgor necessary for spore discharge.

It is interesting to compare the xerophytism of *Ganoderma applanatum* and *Fomes fomentarius* with that of the pyrenomycete *Daldinia concentrica*. In all spore discharge occurs during the summer when the air is driest. In all discharge goes on irrespective of rain or humidity. But in *Daldinia* there is a water reserve in the stroma which is gradually used up, whilst in the perennial polyphores the reserve is in the wood.

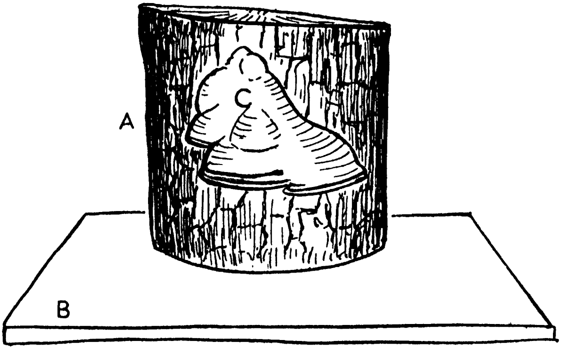

FIG. 52. Specimen of *Fomes fomentarius* (*C*) on a detached segment of poplar trunk (*A*) placed on a table (*B*) in a museum. From a photograph by Buchwald (1938).

Light. In general, light appears to exert little direct influence on spore liberation in Hymenomycetes. Most workers have reported discharge as occurring day and night throughout the whole spore-fall period in agarics and bracket fungi. Recently, however, *Corticium filamentosa*, which forms its basidia on the leaves of *Hevea*, has been shown to be nocturnal in its spore discharge.* Again, in small toadstools with a spore-fall period of only a few hours the production of fruit-bodies and, therefore, the liberation of spores may be periodic. Thus, in *Coprinus curtis* sporophores mature and shed their spores in the morning, those of *C. plicatilis* from midday to early afternoon, and those of *C. fimetarius* from midnight to dawn.†

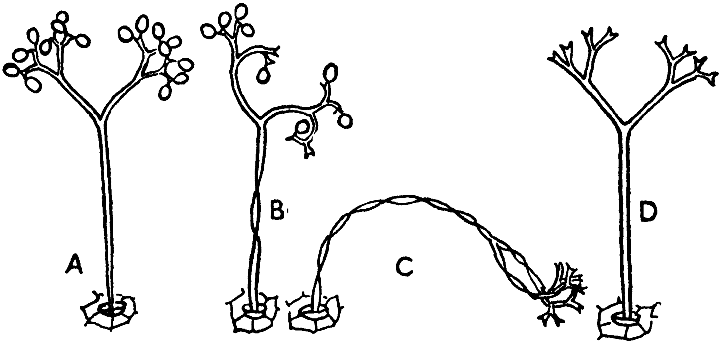

FIG. 53. *Peronospora tabacina.*

A, conidiophore in damp air with attached conidia; *B* and *C*, changes on exposure to air of low humidity; *D*, recovery when returned to damp air. After Pinckard (1942).

Discharge due to hygroscopic movements

Liberation of spores from branched conidiophores by the hygroscopic movements of the main axis was described long ago by de Bary.‡ He said:

> Where filiform sporophores rise free into the air, a further mechanical arrangement is found which greatly assists the shedding and scattering of the abscised spores. It may be readily observed in the Hyphomycetes, in *Peronospora*, *Phyto-*

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* Carpenter (1949).

† Buller (1924 and 1931).

‡ de Bary (1887).

phthora infestans, and in the gonidiophores of *Peziza fuckeliana*,* &c. The hyphae of these fungi are cylindrical in the moist and turgescent state, but collapse when dry and especially when the spores are ripe into a flat ribbon-like form, and the drier they are the more strongly do they become twisted round their own longitudinal axis. They are so highly hygroscopic that the slightest change in the humidity of the surrounding air, such for instance as may be caused by the breath of the observer, at once produces changes in their turgescence and torsion; the latter give a twirling motion to the extremity of the gonidiophore, and the ripe spores are thereby thrown off in every direction.

More recently it has been described and figured for *Peronospora tabacina* by Pinckard† (Fig. 53), whose account agrees closely with that of de Bary. However, in downy mildews and their like the ripe spores are very finely attached and easily blown off their conidiophores by wind, so that the biological importance of hygroscopic discharge seems very uncertain.

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* Now *Sclerotinia fuckeliana* (de Bary) Fuckel.

† Pinckard (1942).

III

SPORES IN THE AIR

GROWTH of moulds on damp bread, moist leather, and decaying vegetable matter must have been familiar to man from early times, but the recognition of these growths as fungi came only with the use of the compound microscope. Robert Hooke, the first of the great microscopists, seems to have been the earliest to suggest (1665) that moulds are 'nothing else but several kinds of small and variously figur'd Mushrooms', but even when recognized as fungi they were still generally regarded merely as by-products of organic decay without the power of reproduction. Clear evidence that these organisms develop from 'seeds' was given by Micheli (1729) who not only observed the microscopic 'seeds', but also showed by experiment that they could reproduce the species. The 'seeds' were, of course, spores, but the academic distinction between seeds and spores was made much later by Hedwig in 1789. Spallanzani (1777), arguing from well-conceived controlled experiments, threw additional doubt on the generally accepted view of spontaneous generation and pointed out that the apparently spontaneous development of moulds was probably due to the omnipresence of their spores. He wrote: 'The seeds of mould may be disseminated in such abundance as to enter into the composition of all animal and vegetable substance . . . it is the readiest method of accounting for the extraordinary abundance and universal existence of mould.' Later (1865) Pasteur proved, in so far as a negative can be proved, that neither fungi nor bacteria are generated spontaneously, but that their reproductive units normally occur in air, so that following brief exposure any suitable sterilized nutrient develops colonies of bacteria, yeasts, and moulds.

The spore content of the air has been extensively studied in modern times. It is a matter of prime concern to the mycologist studying the epidemiology of plant diseases, and recently, on the medical side, the importance of fungal spores in the air has been emphasized in connexion with inhalent allergy.

Before discussing the main facts about the occurrence and distribution of fungal spores in the air, it is necessary to examine the principal experimental methods that have been used.

The student of spores in the air, whether he is concerned with spores as allergens or with the spread of plant pathogens, is interested not only in what kinds are present but also in their concentration. Consequently the best methods would seem to be those in which the number of spores per unit volume is directly determined. As early as 1887 Frankland,* developing a method used by Pasteur,† attempted determinations of this nature. A known volume of air was aspirated through a tube stuffed with gun cotton. This was later dissolved in an ether-alcohol mixture and the spores in the liquid were counted. A modern form of this method, developed in connexion with the analysis of particle size in fogs and aerial dusts, is the cascade impactor.‡ This apparatus is illustrated in Fig. 54. The whole outfit with its wind-vane attachment is suspended by its centre of gravity in such a way that it can turn freely so that the plane of the first greased slide faces the wind. Air is sucked through the apparatus at a definite rate. It is found that the speed of intake should be approximately the same as the velocity of the wind, for if not the lines of flow of the air-stream entering the impactor are considerably distorted,

* Frankland (1887). † Pasteur (1862). ‡ May (1945).

leading to important errors. The larger particles are deposited on the first slide, smaller ones on the second, and so on. The range of particle size trapped on each slide depends on the shape and density of the particles and on the rate of inflow of air into the apparatus. With an intake of 17·5 litres a minute and with particles having a density of 1·0, slide I traps those of diameter 5·5–20 μ, slide II 1·5–7 μ, slide III 1–3 μ, and slide IV 0·3–1·5 μ. Clearly most fungal spores would be impacted on the first two slides. After the apparatus has been in operation for the required time, the slides are removed and examined microscopically and the spores on each are counted. Thus, knowing the volume of air that has been sucked into the apparatus, the

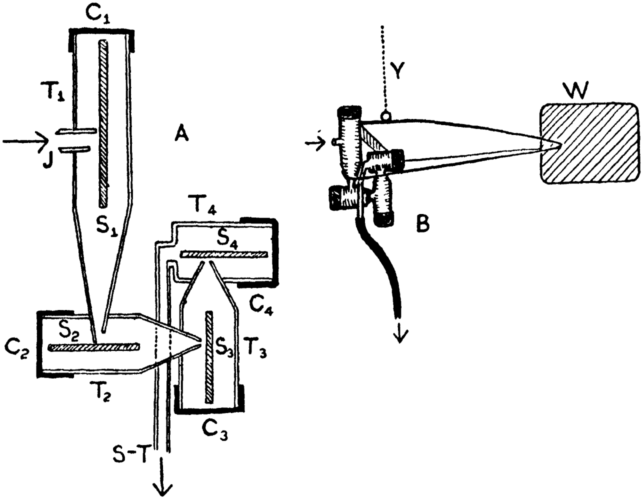

FIG. 54. Cascade impactor.

_A_, diagram of apparatus seen in longitudinal section; _J_, entry jet; S_1–S_4, greased sampling slides; T_1–T_4, brass tubes fitted with movable caps (C_1–C_4); _S–T_, suction tube; _B_, whole apparatus on smaller scale, showing the wind-vane attachment (_W_) and the thread (_Y_) by which the apparatus is suspended. Based on May (1945). Arrows show movement of air-stream sucked through the apparatus.

concentration of each recognizable kind of spore in the air can be calculated.

The gravity-slide method has been widely used,* especially by allergists, in estimating the pollen-grain and spore content of air. In this a horizontal slide is exposed, protected from rain but otherwise so placed that air has free access to it (Fig. 55). After a period of exposure a defined area of the slide is examined microscopically, the spores identified, if possible, and counted. The merit of this method is its extreme simplicity. However, since those studying spores in the air are concerned primarily with the number present in unit volume, the gravity-slide method is justified only if there is a reasonable correlation between spore deposition and spore concentration. No such correlation has been found to exist. Thus Buller and Lowe† in an

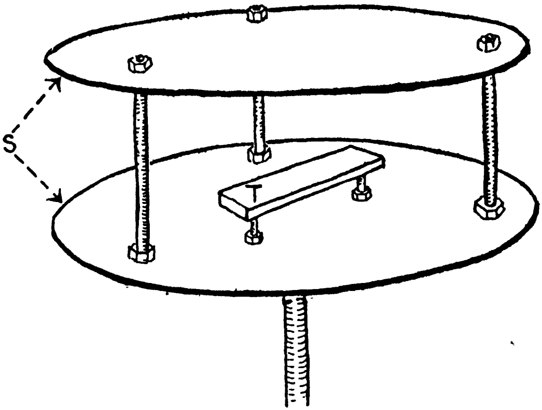

FIG. 55. Gravity-slide method for sampling spores in the air. *S*, shelter consisting of two metal disks spaced apart; *T*, table on which greased sampling slide is placed. After photograph by Durham (1944).

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* Durham (1946); Hyde and Williams (1945).

† Buller and Lowe (1910).

investigation of the micro-organisms present in the air of Winnipeg throughout the year found that the ratio:

$$\frac{\text{micro-organisms deposited per sq. foot per min.}}{\text{micro-organisms in 10 litres of air}}$$

varied between 3 and 283, and much more recently Durham* found, in the course of an extensive study, that the ratio of the gravity to the volumetric catch varied from 7 to 223. In perfectly still air, no doubt, the number of spores reaching a horizontal surface would be proportional to their concentration in the air, but normal air is not still but is of ever-changing turbulence, and most of the spores coming to rest on a surface do so by 'impaction' rather than by steady fall under the influence of gravity. Thus the gravity-slide method can be considered to give only rough quantitative information about the spore content of the air. Some workers have used vertical greased slides mounted on a wind-vane so that the wind may always impinge directly on the surface of the glass. This was the method employed long ago by Cunningham† in his aeroscope. It has been used in this country for the study of atmospheric pollen‡ and in connexion with the epidemiology of rust in Canada.§ Here again the catch can bear little relation to the number of spores in unit volume of air, especially as the volume of air impinging on the slide must vary with the velocity of the wind.

When spores are caught on a slide and examined microscopically, the fundamental difficulty of the method is identification. Rarely are specific determinations possible, and the genus, family, order or even class may be impossible to ascertain when the spores, as are so many fungal spores, are small, unicellular, and hyaline. However, in some genera

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* Durham (1944).

† Cunningham (n.d. but *c.* 1873).

‡ Hyde and Williams (1945).

§ Craigie (1945).

the spores are large and unmistakable (e.g. in *Helminthosporium* and *Alternaria*). The uredospores of rusts and the spore-chains of *Cladosporium* are also easy to identify.

Some workers use petri dishes containing sterile nutrient agar as spore-traps.* When sampling is done at or near ground level, the sterile agar surface is briefly exposed in a horizontal position, but when exposures are made from aeroplanes the dish is exposed vertically and facing forwards so that spores are impacted on the agar.† Following exposure the dishes are incubated and after several days an attempt is made to identify the fungal colonies that develop. An outstanding objection is that obligate parasites, especially rusts and downy and powdery mildews, do not figure in counts made by this method. Further, many slow-growing saprophytes are swamped by more vigorous species before they can form visible colonies. Again, the results obtained depend on the nature of the nutrient medium, since one type of medium may favour the growth of certain species more than others.

It is noteworthy that none of the usual methods normally reveals the presence of the basidiospores of the larger fungi in the air. They grow too slowly to be recorded in the exposed petri-dish method, and they are not sufficiently characteristic to be identified microscopically when caught on a greased slide; yet at certain times of the year spores of the larger fleshy fungi presumably form a significant part of the aerial plankton.

Those who have used the exposed petri-dish method in investigating the spore population of the air have usually found that the most abundant species are dry-spore moulds such as species of *Cladosporium* (especially *C. herbarum*), *Alternaria*, *Penicillium*, *Botrytis* (*B. cinerea*), *Sporotrichum*, and *Epicoccum*. But in addition a few colonies of slime-spore

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* Horne (1935).

† MacLachlan (1935).

fungi such as *Mucor* spp., *Phoma* spp., and *Fusarium* spp. usually make their appearance on exposed plates. This is understandable, for although in slime-spore species the spores are not liberated directly into the air, they may, after a primary dispersal by rain or some other agency, become associated with dry soil or other particles and these may become suspended as dust in the air. However, the preponderance of dry-spore types in the air is unmistakable. In an extensive investigation carried out by Horne* at two separate localities the ratio of dry-spore colonies to slime-spore ones was 24: 1 at Swanley and 28: 1 at East Malling.

Investigators who have examined exposed sticky slides have been particularly struck by the abundance of spores of *Alternaria* spp. at certain times of the year in some regions, and great attention has been given by allergists to spores of this genus because there is clear evidence that people may be allergic to them and because they are so easy to identify. A thorough study has been made of the seasonal fall of *Alternaria* spores at over fifty stations scattered throughout the United States.† The fall is heaviest in the great agricultural areas, especially in the zone of the Mississippi valley, and comparatively slight in the western states. *Alternaria* occurs as a very common saprophyte on old straw and its local abundance depends on the presence of this substratum in sufficient amount. Again, as is to be expected, the frequency of the spores in the air varies from season to season. Thus in South Wales‡ the spores are abundant in the air during summer months but relatively rare at other times. Sometimes the fall of *Alternaria* spores may be on a remarkable scale. An extreme example is the great spore-shower recorded in America† between 6 and 8 October 1937. Spores rained down over the whole eastern

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* Horne (1932).

† Durham (1942).

‡ Hyde and Williams (1946).

area of the United States and at some places the deposition on horizontal slides reached 800–1,200 per sq. cm. per day.

Seasonal fluctuations in the spore content of the air have

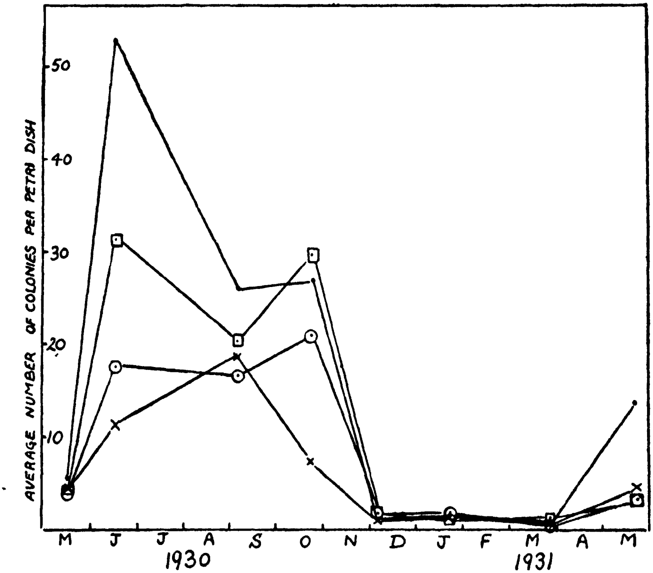

FIG. 56. Seasonal occurrences of spores in the air. Each graph is for a separate site at Swanley and each point is an average based on ten exposed petri dishes. Data from Horne (1935).

been noted by all workers who have pursued their researches over the course of a year. Horne,* for example, exposed petri dishes containing nutrient agar on stands 10 feet from ground level at Swanley. For each determination ten dishes were used, exposed for three minutes and examined for fungal colonies after several days' incubation. Four distinct sites were studied, three in an orchard

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* Horne (1935).

and the other on arable land. The results for each site are illustrated in Fig. 56. It is clear that during the summer and autumn spores were relatively abundant in the air, but during the winter there were very few. Here again the seasonal variations of spores in the air doubtless correspond with the seasonal development of the fungi, although day-to-day fluctuations in counts, which may be very considerable, are probably connected with current meteorological conditions influencing spore liberation, dispersal, and deposition.

Since fungi with air-borne spores are land organisms, one would expect the air over the sea to become progressively freer from spores on receding from the land, and this is clearly indicated by data obtained* by exposing petri dishes at mast-head level on a ship at increasing distances from the shore. Over the sea in mid-ocean the air may be almost free from fungal spores, but not from bacteria, since marine species are continually replenishing the bacterial population of the air in spray from the crests of breaking waves.

The question of the distribution of spores in the upper air first came into prominence in connexion with the epidemiology of cereal rusts. Plant pathologists were anxious to know if viable uredospores were to be found there in sufficient abundance to spread infections to distant regions. The pioneer work on this problem was carried out under the leadership of Stakman,† who has contributed so much to the study of rust epidemiology in America. Sticky slides were exposed from an aeroplane operating at varying heights. In June and July, over the wheatlands of the Mississippi valley at heights up to 11,000 feet, spores were found to be relatively abundant, those of *Alternaria* being

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* Zobell (1942).

† Stakman, Henry, Curran, and Christopher (1923).

by far the commonest, with uredospores of cereal rusts next in frequency, followed by the conidia of *Helminthosporium* (Table 2). All these could be recognized with reasonable certainty, but there were many besides which could not be identified. Many of the spores were viable. Thus *Alternaria* conidia caught at altitudes up to 10,500 feet and uredospores trapped at 7,000 feet germinated readily, indicating their ability to withstand the conditions of desiccation, insolation, and temperature obtaining at these altitudes. Since 1923 many workers, usually with the aid of aeroplanes, have studied the spore content of the air far above ground level, and their results in the main confirm Stakman's conclusions without adding any important facts. Mention may be made, however, of the trapping of spores belonging to several genera of Fungi Imperfecti above 36,000 feet by a sampling apparatus released from the stratosphere balloon *Explorer II.**

TABLE 2

Extracts from Table by Stakman et al. (1923)

Slide No.	*Date*	*Altitude in feet*	*Length of exposure (minutes)*	*Uredospores of stem and leaf rusts*	Alternaria *conidia*	Helminthosporium *conidia*	*Miscellaneous spores*	*Pollen grains*	*Total*
6	29 April	500–1,500	30	355	1	1	3	21	381
14	28 April	16,000–16,500	10	2	..	..	..	..	2
19	23 May	1,000–2,000	30	166	36	1	15	..	218
24	,,	11,000–12,000	5	9	1	..	..	..	10
28	,,	3,000	30	136	35	3	25	4	203
31	13 July	6,000	25	7	34	3	14	12	70
36	15 ,,	2,500	20	2	19	..	18	1	40
47	23 ,,	5,000–7,500	35	11	57	1	50	25	144

In recent years plant pathologists have given considerable attention to the question of the dispersal of airborne spores around a centre of liberation in an attempt to

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* Rogers and Meier (1936).

define the size of the danger zone around a locus of infection. An important contribution to this subject was made by Stepanov.* In one of his experiments he liberated slowly through gauze at a certain point approximately $1 \cdot 2 \times 10^9$ spores of the smut *Tilletia caries* at a height of 1 m. above the ground, the wind at the time varying from 0 to 4 metres per second. The spores were trapped on glycerine-coated slides at different distances from the source in the general leeward direction. The results of this particular experiment are given in Table 3. The striking feature of this work was the demonstration of the very steep gradient in spore deposition on receding from the source. This seems to be a fairly characteristic feature of wind dispersal (Fig. 57). For example, data for aecidiospores caught on

TABLE 3

Number of spores of Tilletia caries *deposited on horizontal cover-glasses (18×18 mm.) at varying distances from point of spore liberation in the general down-wind direction, but at varying angles to the wind*

Each figure is the average of two exposed cover-glasses

Angle to wind	*Distance from source in metres*			
	5	*10*	*15*	*20*
−20°	204	23	4	0
−10°	435	45	19	8
+30°	964	212	207	49
+45°	1198	587	87	142
+55°	659	123	77	15
+65°	341	24	26	7
+75°	365	5	26	53
+85°	20	10	9	14
Average	523	129	57	36

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* Stepanov (1935).

vertical greased slides at increasing distances from a barberry hedge heavily infected with *Puccinia graminis* tell the same story.* Again, the same dispersal pattern is evident if

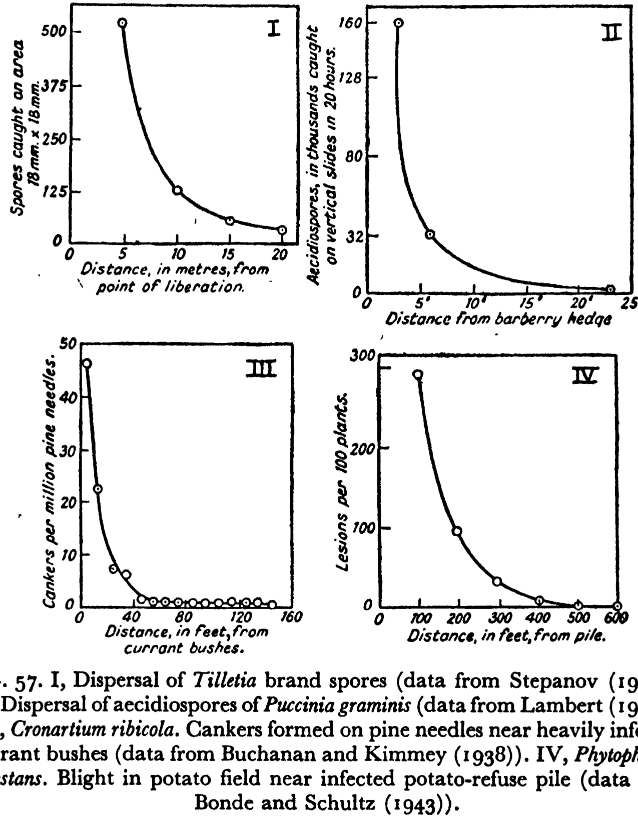

FIG. 57. I, Dispersal of *Tilletia* brand spores (data from Stepanov (1935)). II, Dispersal of aecidiospores of *Puccinia graminis* (data from Lambert (1929)). III, *Cronartium ribicola*. Cankers formed on pine needles near heavily infected currant bushes (data from Buchanan and Kimmey (1938)). IV, *Phytophthora infestans*. Blight in potato field near infected potato-refuse pile (data from Bonde and Schultz (1943)).

one considers the degree of infection of plants at increasing distances from a source of air-borne inoculum. Thus in the attack on pines by the heteroecious rust *Cronartium ribicola* it

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* Lambert (1929).

has been found* that in trees around rusted currant bushes the percentage of infected needles declines so rapidly with distance that beyond 60 yards from the bushes the pines are infected to a negligible degree. Potato blight may present a similar picture.† In parts of the United States the first infection of potato fields by *Phytophthora infestans* is due to conidia developing on shoots derived from diseased tubers on old potato-refuse piles. A study of primary infection in a potato field adjoining such a pile showed clearly that the number of blight lesions per 100 plants decreased rapidly with distances. Many similar examples could be cited.

In general it is clear that even if spores are liberated at a point by the thousand million, the number falling on a small area a mile away may be almost negligible. This, perhaps, helps us to understand the enormous spore production of so many fungi. However, although the general picture is clear, more exact information is needed about dispersal around a centre using more satisfactory methods of determining the actual spore concentration in the air at increasing distances.

The theoretical basis of spore dispersal in the air has been considered by a number of workers. Some consider that the wind velocity and the rate of fall of spores in still air are the essential features determining dispersal. This rate of fall varies from 0·05 cm. sec. for the minute spores of *Lycoperdon pyriforme* (4·2 μ diam.) to 2·8 cm. sec. for the large elongated conidia of *Helminthosporium sativum* ($29 \times 68\,\mu$), but for most fungal spores it is of the order of 1 cm. sec. It has been calculated‡ that if a spore of *Ustilago zeae* fell by its own weight after attaining a height of 1 mile in the air and if the wind blew at 20 m.p.h., it would be borne

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* Buchanan and Kimmey (1938).

† Bonde and Schultz (1943).

‡ Christensen (1942).

to a distance of about 2,500 miles in the nine days of its descent to earth. A number of similar calculations have been made, but they seem to be of little or no significance* since an all-important property of the air—its turbulence—is ignored. It is quite clear that individual spores can be carried for hundreds or even thousands of miles by strong winds, but it is doubtful if the rate of fall in still air has anything to do with the distance of transport. Further, what is of most concern to the student of plant pathology is not the occasional transport of individual spores to very great distances, but rather the normal distance of effective dispersal.

Since the wind is so capricious in its behaviour, it may well be doubted if any quantitative generalizations can be made about dispersal, but Gregory* has pointed out that 'the problem is statistical because, whilst the destination of a single spore in a wind eddy is inscrutable, the average distribution of vast numbers of spores over a uniform area and over a period of time offers hope of rational treatment'. He applies the modern meteorological concepts of eddy diffusion to the problem and develops a somewhat elaborate formula to describe dispersion around a point source, but the great advance of his formula over those of others is that the constants used are not arbitrary, but have a defined physical significance. Further, reviewing the experimental results of many workers, Gregory finds a reasonable correspondence between theory and fact.

A rough picture of dispersal by wind and eddy-diffusion can be obtained by watching the smoke-trail from a factory chimney. It tends to be conical with the apex at the chimney's mouth and the smoke cloud is visibly turbulent. At the periphery eddies are continually mixing the smoke cloud with smoke-free air, thereby increasing the width of

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* Gregory (1945).

the cloud and diluting it. In connexion with this conical model of dispersal experiments by Wilson and Baker* are of interest. As a convenient experimental material they used spores of the club-moss *Lycopodium*. Large numbers of spores were liberated over a period of fifteen minutes at a point 7½ feet above the ground and trapped to leeward on vertical greased slides exposed 5, 10, and 15 feet away at a series of heights varying from 1·5 to 13·5 feet. The results of one of their experiments are shown diagrammatically in Fig. 58. The conical pattern of dispersion is clearly to be seen. It has been pointed out that if wind dispersal is of

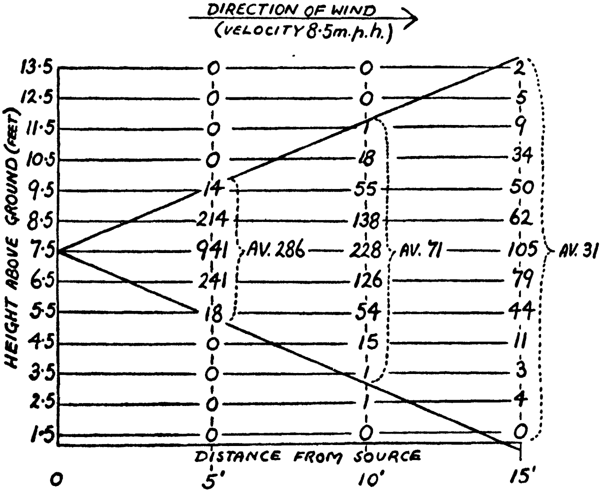

FIG. 58. Diagram showing the results of one of Wilson and Baker's experiments on the dispersal of *Lycopodium* spores. Spores set free 7·5 ft. above ground and caught down-wind on greased vertical slides at various heights and 5, 10, and 15 ft. away. Figures give catch on 1 sq. cm. greased slide. Lines have been drawn showing that nearly all the trapped spores are contained within a cone with its apex at the point of liberation.

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* Wilson and Baker (1946).

this conical type, the average concentration of spores at cross-sections of the cone should be inversely proportional to the square of the distance from the source. In the experiment depicted in Fig. 58 this is clearly so, although the spore concentration along the axis of the cone is greater than near its surface.

In considering gradients of spore concentration on receding from a source attention has been focused on horizontal gradients, but there are vertical gradients as well. Vertical distribution has been studied by collecting spores on sticky surfaces exposed from aeroplanes operating at different heights. Stakman and his colleagues found in a general way that the greater the altitude the fewer the spores, and this has been borne out by later workers. Two examples may be given. The rust *Gymnosporangium juniperi-virginianae* attacks cedars, forming galls bearing the teleutospore stage. Following rain, basidiospores are discharged in enormous numbers. From an aeroplane flying at about 85 m.p.h. over a heavily infected area of red cedar, petri dishes containing agar were exposed for a standard time. These dishes were later examined and the trapped spores counted (Table 4). Again, Craigie* exposed greased slides in Manitoba above wheatfields heavily infected with stem rust. Each slide was exposed from an aeroplane for ten minutes and the number of uredospores caught on one square inch was counted (Table 5). These vertical gradients of spore concentration are of considerable interest since they help to explain the efficacy of certain physical barriers to the spread of air-borne disease. Thus a mountain chain may protect an area of wheat from uredospores originating in a neighbouring country, since the vast majority of the spores, being in the lower levels of the air, are precipitated on to the mountain-sides.

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* Craigie (1945).

TABLE 4

(Data from MacLachlan 1935)

Height ft.	*Basidiospores per petri dish*	*Average*
100	12 29 20 17	19·5
500	8 12	10·0
1,000	2 2	2·0
1,500	0 0	0
2,000	0 0	0

The principal fact emerging from a study of wind dispersal from a centre is that it is essentially local, and plant pathologists find that the practical safety zones around centres of infection are remarkably small. However, the spread of cereal rusts calls for special attention, since in certain regions long-distance infection on a considerable scale may frequently occur.

TABLE 5

Date	*Number of uredospores per sq. inch intercepted by microscope slides at different heights: 10 minute exposure*			
	1,000 ft.	*5,000 ft.*	*10,000 ft.*	*14,000 ft.*
5 Aug. 1930 .	24,200	7,560	108	10
10 Aug. 1930 .	24,000	170	36	30

During the past quarter of a century the epidemiology of black stem rust of wheat caused by *Puccinia graminis tritici* has been extensively studied on the North American continent where there is a more or less continuous belt of wheat cultivation spreading northwards from Mexico through the Mississippi valley to western Canada. Infection of the wheat in early summer may be by aecidiospores from local barberry bushes, by uredospores that have survived the winter, or by air-borne uredospores coming from far away. In west Canada barberry is rare, the coldness of the winter normally prevents the survival of uredospores, and it seems, therefore, that the early primary infection of the wheat is largely due to uredospores blown from the far-away warmer south, where the fungus develops earlier.

In connexion with the epidemiology of black stem rust Craigie* has made a long-term study of uredospores in the air at a number of stations in western Canada. The technique used was to expose at each place for one or two days a vertical sticky glass slide mounted on a vane so that it continually faced the wind. It was found that viable spores occurred in the air of Manitoba for a week or two each year *before* any infections could be seen in the field. Sometimes the vaselined slides showed sudden but temporary increases in uredospore deposition associated with 'spore showers'. Such a shower was usually followed, after a necessary incubation period of a week or two, by the development of stem rust on the wheat in the neighbourhood. It is of interest to consider an unusually early and rather spectacular example that occurred in 1929. Records for 12 June to 28 June are given in Table 6. The actual shower occurred between 16 and 18 June, and from 12 to 19 June a south wind prevailed. The evidence suggested

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* Craigie (1945).

that the uredospores came from a region of the Mississippi valley at least 500 miles away, since at this time the northern limit of rusted wheat was approximately along the line shown in Fig. 59. Another equally remarkable instance is cited by Stakman and Christensen.* Early in June 1925 black stem rust was general in the wheat-growing region south of lat. 40°, but not north of this parallel. In the first week of June, however, strong winds blew from the south and by 10 June rust had appeared in nearly all fields of susceptible wheat up to 600 miles north of lat. 40°, reaching almost to the Canadian border. Thus early in the rust season, apparently, a great shower of uredospores spread infection almost simultaneously over an area of nearly a quarter of a million square miles.

TABLE 6

Date	*Number of Stem Rust uredospores caught each two-day period on 1 square inch of sticky glass surface at*		
	Morden	*Winnipeg*	*Brandon*
12 June . .	0	0	0
14 " . .	0	0	0
16 " . .	24	133	0
18 " . .	174	193	68
20 " . .	0	0	0
22 " . .	0	0	0
24 " . .	0	0	0
26 " . .	0	0	0
28 " . .	15	1	0

As well as the infection of northern regions in early summer by uredospores from the south, a reverse infection may occur in autumn. Uredospores often fail to survive the hot summer in the south (e.g. in Texas), but the young winter wheat may be infected in early autumn by uredospores

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* Stakman and Christensen (1946).

blown southwards from rusted areas hundreds of miles to the north.

The long-distance dispersal of rust spores in America and in the other great wheat regions of the world raises the question of whether it is different in kind from the local dispersal around a centre which has already been discussed. It is difficult to answer this question with confidence, but it should be noted that the uredospores certainly do not come from a 'point' source, but perhaps from an area of rusted wheat of several thousands of square miles, and a rusted crop may develop an astronomical number of spores. 'On an acre of slightly rusted wheat there may be 10,000,000,000,000 uredospores and several times this number on an acre of heavily infected grain.

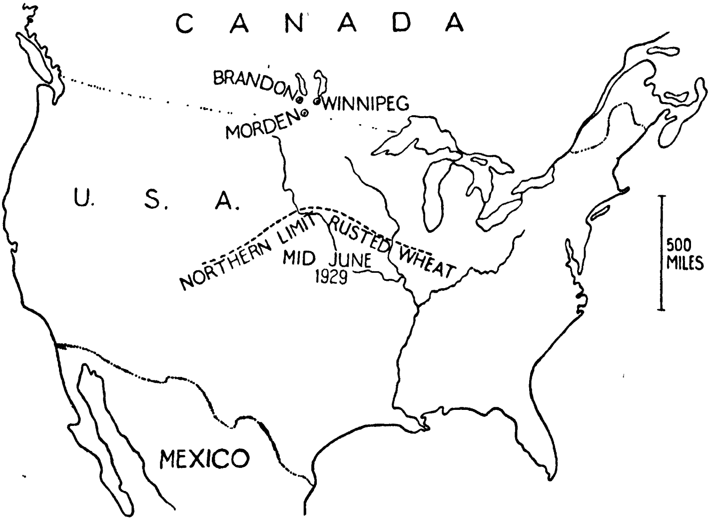

Fig. 59. Sketch-map of N. America showing northern limit of rusted wheat in mid-June 1929, when a very early shower of uredospores fell in western Canada at Brandon, Morden, and Winnipeg.

Indeed, clouds of "rust dust" can often be seen rising into the air when heavily infected wheat is being harvested; and machines, men and soil are often red with countless numbers of spores.'*

The long-distance dispersal of the uredospores of black rust in America raises the question of the possible inter-continental spread of plant diseases by air-borne spores. For example: are viable spores air-borne from America to Europe and vice versa? This is still an open question, although the available evidence suggests that the Atlantic acts as an effective barrier to the spread of air-borne plant diseases. More information about the spore content of the air over mid-ocean would be extremely interesting in this connexion.

The complete dispersal story of an air-borne fungus involves not only the liberation if its spores and their actual passage through the air, but also their deposition. This matter has recently been considered in some detail by Gregory.† Two processes can be recognized: (1) *impaction* on a surface due to the momentum of a wind-driven spore, and (2) *sedimentation* under the influence of gravity. A study of impaction on sticky vertical cylinders of *Lycopodium* spores blown through a wind-tunnel showed that the number of spores caught per unit area increased greatly with decrease in the diameter of the cylinders from 2·0 cm. to 0·018 cm. Similar results were obtained outdoors on trapping air-borne fungal spores above a field of grass. A consideration of impaction in relation to spore size led to the conclusion that, although larger spores may frequently be impacted on a stem or leaf, the smaller ones can rarely be brought to rest on such surfaces by this means. They may come to rest on a stem or leaf by sedimentation when

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* Stakman and Christensen (1946).

† Gregory (1951 and 1952).

the air is still or be deposited with falling rain. In connexion with the greater efficiency of impaction of larger spores, Gregory drew attention to the interesting fact that most air-borne leaf parasites have relatively large spores (e.g. rust uredospores, conidia of downy and powdery mildews, spores of *Helminthosporium*).

IV

DISPERSAL BY INSECTS

IT is one of the most striking facts of botany that transport of pollen grains in angiosperms from flower to flower is largely the work of insects, and this reliance on insects has apparently been a major factor in the evolution of floral structures. Although there are a number of interesting examples of spore dispersal by insects, fungi have tended largely to be anemophilous and only in one small family—Phallaceae—is the sporophore as intimately related to insect visitors as is the coloured, scented, nectar-producing flower so common in angiosperms.

The most familiar British species in Phallaceae is the cosmopolitan stink-horn (*Phallus impudicus*) (Fig. 60) so common in all kinds of woods from June to October. The fruit-body nearing maturity is an egg-shaped structure half-buried in the soil and leaf-litter of the forest floor. Then, usually in the evening, the papery skin (exoperidium) ruptures and, early the following morning, the compressed spongy tissue of the stalk rapidly elongates to a height of 15–20 cm., bearing at its apex a conical cap thickly covered with a greenish-black, sugary slime containing millions of very minute basidiospores. At first no smell is emitted and no insects appear on the scene, but after an hour or so a characteristic fetid odour develops which can be detected many yards away. Flies, especially blow-flies and green-bottles, are attracted from far and wide, and it is a common sight to see the cap of a stink-horn crowded to capacity with jostling insects. In two or three hours the spore-slime is completely removed, leaving the bare white, alveolate cap. Spores are carried on the feet and bodies of the insects and also pass rapidly and appar-

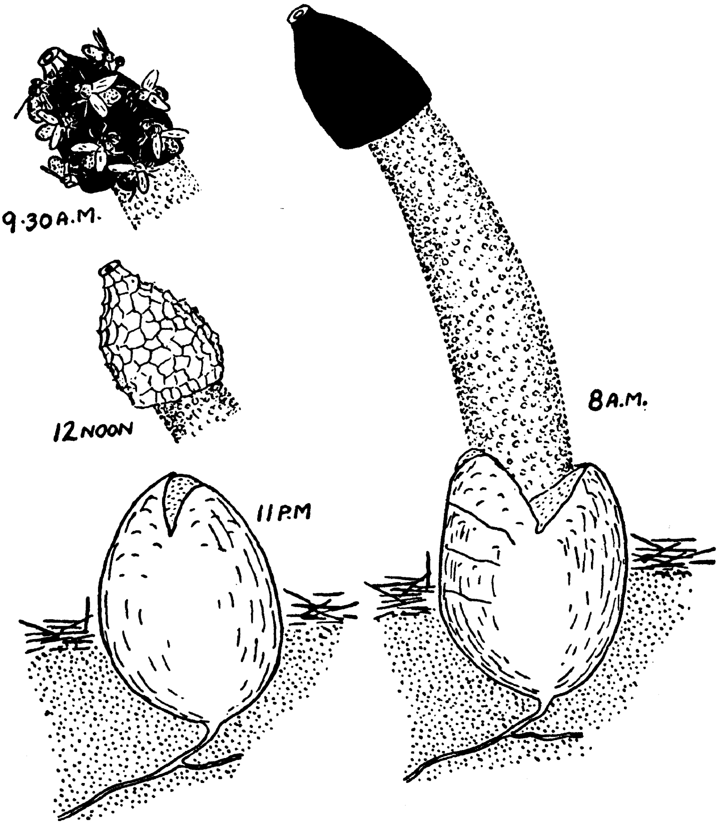

Fig. 60. *Phallus impudicus.*

At 11 p.m. the young fruit-body is at 'egg' stage and the outer papery layer of the peridium has torn, exposing the jelly-like layer below. Next morning at 8 a.m. the stalk has elongated, carrying up the cap bearing the spore-slime and leaving the peridium as a volva around the base. By 9.30 a.m. the slime is giving out a strong smell and has attracted flies, and by noon all the spore-slime has been removed.

ently unharmed through the alimentary canal. However, neither in *Phallus impudicus* nor in any other member of the family has germination of the spores been observed. If the spores have lost their power of germination, effective dispersal of the fungus must be brought about not by the dissemination of basidiospores but by some other means. However, it is more likely that dispersal of this very abundant species is due to transport of basidiospores by insects, but that in the laboratory conditions for spore germination have yet to be realized. In *Mutinus caninus*, very like the stink-horn but smaller and with the cap fused throughout its length to the orange stalk, the odour of the spore-slime is comparatively slight, but *Clathrus cancellatus*, with its beautiful red, spherical network coated with spore-slime, is even more fetid than the stink-horn.

A contemplation of British species of Phallaceae, however, gives but a poor impression of the family, which reaches its richest development in tropical and sub-tropical regions. There are, for example, the beautiful crinoline fungi (*Dictyophora* spp.) agreeing in general form with *Phallus* but having a skirt-like network, often coloured, displayed below the cap around the stalk like a crinoline. Perhaps the most interesting genus from the point of view of dispersal is the Australian *Aseroe rubra*. In this species a sporophore is developed which forms a remarkable parallel with the entomophilous flower (Fig. 61). There is a stipe (peduncle) 2–4 inches long, a central fertile region at its apex where the odoriferous spore-slime occurs, and around this a magnificent 'perianth' of red sterile lobes (petals).

Another example of specialized entomophily is the conidial stage of *Claviceps purpurea*.* This fungus produces its sclerotia (ergots) in rye (*Secale cereale*), rye-grass (*Lolium perenne*), purple moor-grass (*Molinia caerulea*), and, more

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* Atanasoff (1920).

rarely, in other members of Gramineae. Primary infection of the rye apparently is due to filiform ascospores violently discharged during the late spring and borne by the wind to flowers of the host. The fungus invades the ovary, which becomes replaced by a dense mass of fungal tissue which is highly convoluted and covered by a hymenium of simple conidiophores. These produce vast numbers of minute elongated conidia which become involved in a copious, stinking 'honey-dew' in which the sugar concentration may be over 2 molar. The flowers of grasses are not insect-pollinated, but some insects regularly visit the spikelets of rye for the sake of pollen. Others are attracted by the 'honey-dew' secreted by the leaf-louse, an insect found abundantly on the fertile spikes of rye. Insects, especially *Melanostoma mellina*, which feeds both on pollen and on 'honey-dew' whether of insect or fungal origin, seem to be normal vectors of the ergot disease. The spores may be carried on the surface of the insect or they may be sucked in with the spore-containing honey-dew, to be excreted or regurgitated later, perhaps on a healthy spikelet.

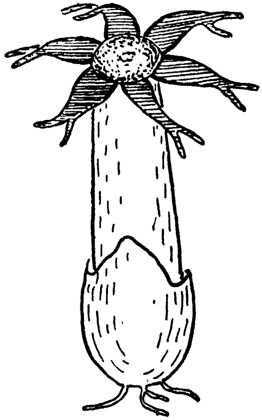

FIG. 61. *Aseroe rubra*. After Cooke. The 'perianth segments' shown with horizontal shading are actually bright red. The slimy spores are associated with the central disk of the 'flower'.

It should be mentioned that, although insects would appear to be the principal agents of the spread of the conidial (*Sphacelia*) stage of ergot, other methods of dispersal may sometimes obtain. In the unnatural conditions of field cultivation conidia may easily be spread by a diseased head knocking against a healthy neighbouring spike, and probably rain-splash as well plays some part in dispersal.

The importance of insects in the dispersal story of rust fungi, though envisaged by Ráthay as early as 1883, was brought into prominence by the brilliant work of Craigie* who demonstrated that *Puccinia helianthi* and *P. graminis* are heterothallic (self-incompatible). This condition has since been shown to occur in many more rusts belonging to a wide range of genera (*Cronartium*, *Melampsora*, *Gymnosporangium*, *Phragmidium*, *Uromyces*). Indeed, self-incompatibility seems to be the normal state of affairs and, according to Buller,† it probably obtains in all rusts with fully developed pycnidia. Homothallic (self-compatible) rusts seem few in number, and in them the pycnidia are rudimentary or absent.

On germination of the teleutospore of *Puccinia graminis* uninucleate basidiospores (sporidia) are produced. These are violently discharged and, being further dispersed by wind, normally fall singly on the leaves of the host. If a basidiospore infects a leaf of barberry, a localized intercellular mycelium is produced on which pycnidia are formed, mainly at the upper surface, and also spherical proto-aecidia embedded in the somewhat hypertrophied leaf tissue near the lower surface.† Each pycnidium (Fig. 62) is more or less flask-shaped, with its wall of interwoven hyphae within the host tissue but with its ostiole, surrounded by a fringe of stiff red, projecting periphyses, opening to the outside. Within the pycnidium minute pycnidiospores are abstricted and ooze out through the ostiole together with nectar, so that each pycnidium is capped by a little sugary drop having an osmotic pressure of between 12 and 24 atmospheres. Often at a later stage the

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* Craigie (1931).

† Buller (1950).

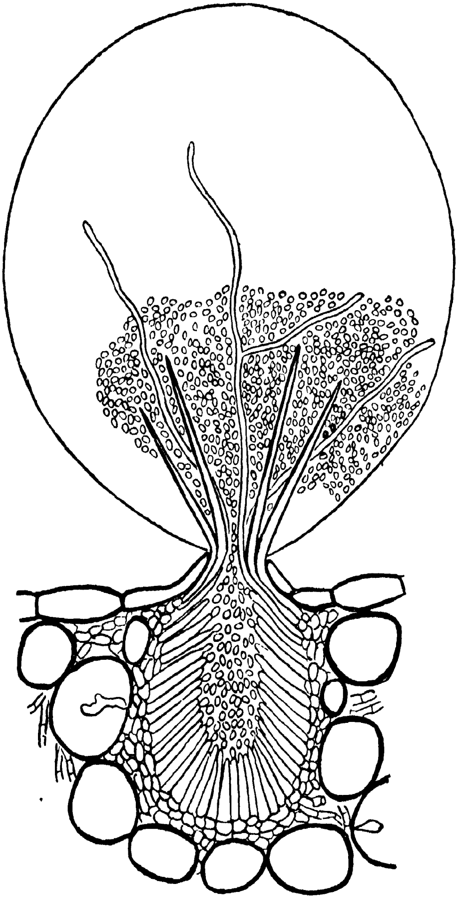

FIG. 62. *Puccinia graminis*. Single pycnidium. The nectar drop contains numerous exuded pycnidiospores, and projecting into it are stiff, thick-walled, red periphyses and the thin-walled and sometimes branched flexuous hyphae. After Buller (1950).

drops from neighbouring pycnidia flow together to form a single larger drop. In addition to the coloured periphyses there project into the nectar-drop through the ostiole a few rather long 'flexuous hyphae' which are simple or sparingly branched and non-septate.

Apparently in most rusts there is a sweet scent associated with the pycnidial stage. This may most easily be detected in the common thistle rust (*Puccinia suaveolens*) which causes a systemic infection of *Cirsium arvense*. Early in the growing season the under surfaces of the leaves of infected shoots are densely covered with pycnidia. The diseased leaves have a scent, almost like that of violets, which disappears when the succeeding uredospore stage develops and the pycnidia disappear. In such a rust as *Puccinia graminis*, where only small local infection spots are involved, the number of pycnidia crowded together is very much less and the scent can be detected only by those with a keen sense of smell.

In Craigie's experiments with *P. graminis* and *P. helianthi* infection of a leaf by a basidiospore led to the development of an infected spot bearing pycnidia at the upper surface and spherical proto-aecidia near the lower. These did not normally develop into aecidia if precautions were taken to exclude insect visitors. When, however, the pycnidial nectar from one infection spot was added to the nectar around the ostioles in another single-spore infection spot, mature aecidia developed in a few days, provided the two infections were of opposite mating types.

According to genetical evidence each aecidiospore contains a '+' and a '—' nucleus. A proto-aecidium borne on a '+' or a '—' mycelium must receive nuclei of the opposite sign if it is to develop into an aecidium. The pycnidiospores would seem to act as diploidizing, or more correctly dikaryotizing, agents although the cytological details of the process are still very obscure. When pycnidiospores are added to the drop around the ostiole of a pycnidium of opposite sign, the flexuous hyphae in the drop fuse with the introduced spores. Presumably the nuclei of these spores pass into the flexuous hyphae, thence into the intercellular mycelium, and so to the proto-aecidium. Here dikaryotization of certain cells occurs and it is these that give the chains of aecidiospores.

Craigie has shown that under experimental conditions flies will mix nectar from different monosporidial cultures and so lead to the development of mature aecidia. Very much earlier Ráthay* studied the insect visitors to pycnidial nectar and recorded a large number of insects that were attracted, including flies, beetles, and ants.

An example somewhat similar to rusts is *Coprinus cinereus*.† This coprophilous agaric has the tetra-polar self-incompatibility type of heterothallism that is a feature of most of the larger Basidiomycetes. Each basidiospore gives rise on germination to a primary mycelium of uninucleate cells, and from this mycelium conidia (oidia) are produced on short conidiophores in slimy heads. The primary mycelium can develop into a secondary one bearing fruit-bodies only if it receives nuclei of the appropriate mating type, and one of the ways this can happen is by contact with suitable oidia. It has been shown experimentally in cultures that flies may transport oidia and effect diploidization of a primary mycelium. No doubt this kind of transport is also effective in nature, although diploidization must frequently, perhaps usually, occur following the intermingling of primary mycelia derived from basidiospores of compatible mating types germinating in the same dung ball.

In some pathogenic fungi spore production is in the host flower and dispersal from infected to healthy plants is

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* Ráthay (1883).

† Brodie (1931).

brought about by insects in the course of pollination. The most familiar example is *Ustilago violacea*, the common anther-smut of campions and other members of Caryophyllaceae. Infection of the host is systemic or semi-systemic but spore production is restricted to the anthers. Diseased plants appear almost normal until flowering, when it is found that blackish-purple smut spores are produced in place of pollen grains. In *Melandrium album* there are separate staminate and pistillate plants. When the staminate plant is infected by *Ustilago violacea* the floral structure is modified only to the extent that smut spores are formed in place of pollen. When, however, the pistillate plant is infected the staminal rudiments are stimulated to develop into stamens, but from their anthers brand spores, not pollen grains, are set free (Fig. 63). Further, the ovary is somewhat reduced and although ovules are present they do not develop into seeds. The smutted flowers still give

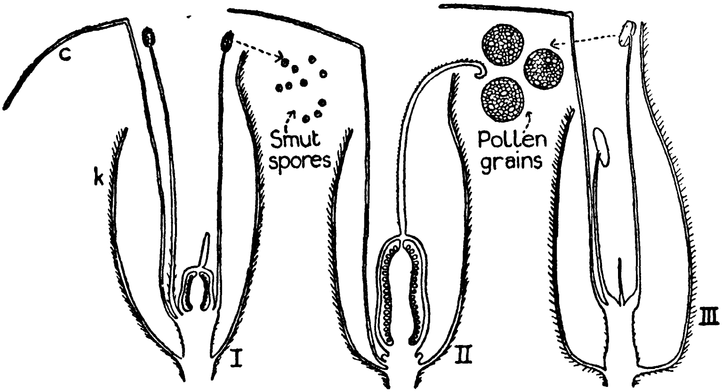

FIG. 63. Flowers of *Melandrium album* seen in longitudinal section.

I, Infected pistillate flower showing stamens (developed from staminal rudiments) containing smut spores; *c*, petal; *k*, calyx-tube. II, Pistillate flower from healthy plant showing staminal rudiments. III, Staminal flower from healthy plant. Smut spores and pollen grains drawn magnified to same scale.

out their scent and are visited by night-flying moths which distribute the spores to flowers of healthy plants. There is conflicting evidence about how infection of the host takes place,* but it seems clear that when brand spores are transferred to a flower on a healthy plant they germinate to produce a mycelium that grows back through the flower stalk into the shoot, so that flowers which develop subsequently on that plant may be smutted. The old view that contamination of a flower by smut spores led to the production of infected but viable seed, as in the loose smut of wheat and barley (*Ustilago nuda*), is not borne out by more recent experiments. Again, infection through the flower is probably not the only method by which the fungus is handed on to healthy plants. There is little doubt that seedling infection also occurs.

Another anther-smut in which the spores are probably dispersed by insects is *Ustilago succisae*, found frequently on devil's bit scabious (*Succisa pratensis*). Here spore production is again limited to anthers. However, the brand spores are white or pale cream in the mass—not black, as in most smuts. Infected flower-heads are easily spotted since the projecting anthers are whitish in contrast to their purple colour in normal plants.

The anther mould of red clover caused by the hyphomycete *Botrytis anthophila*,† shows a remarkable parallelism with the anther smut of campions. The disease is systemic, but spore production is limited to the flowers, the conidiophores of the fungus being produced on the surface of the anthers (Fig. 64). The conidia may be carried by a pollinating bee to the stigma of a healthy flower, where they germinate and the germ-tubes penetrate the tissue of the style after the fashion of pollen-tubes. The developing seeds are infected and within these a dormant mycelium is formed.

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* Baker (1947).

† Silow (1933).

These infected seeds are viable, but in the following year they give diseased plants.

A further example of dispersal of a fungal pathogen by pollinating insects is to be found in endosepsis of figs.* The causal organism (*Fusarium moniliforme* var. *fici*) may be introduced into the edible fig by its obligate pollinator, the fig-wasp (*Blastophaga psenes*). Again, nectar-fermenting yeasts are often carried from flower to flower by bees. For example, *Candida reukaufii*† grows in the nectar of a wide range of flowers. The fungus can be isolated by trapping a bee after it has visited an affected flower, rendering it

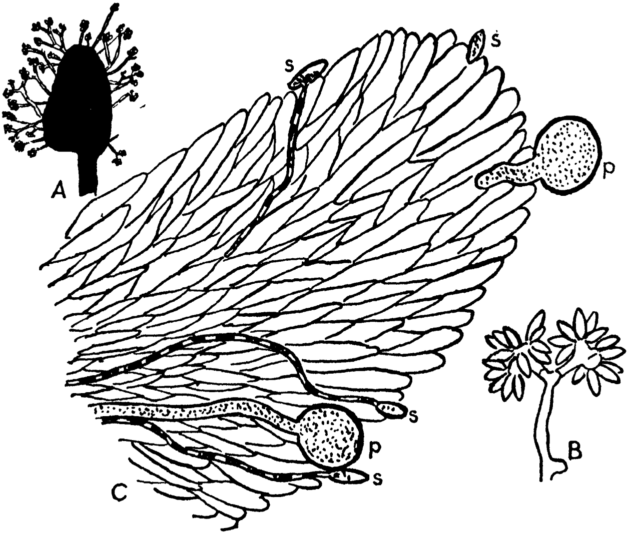

FIG. 64. *Botrytis anthophila*.

A, anther and part of filament from the flower of a diseased clover plant; the anther is covered with the conidiophores of the fungus; *B*, a single conidiophore bearing numerous conidia; *C*, the stigma of a clover flower showing germinating pollen grains (*p*) and conidia (*s*). After Silow (1933).

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* Caldis (1927).

† Grüsz (1927).

unconscious with ether and finally cutting off its proboscis and planting it on nutrient agar (Fig. 65). It is thought that the yeast may spend the winter in the alimentary tract of bumble bees and be introduced into nectaries in the spring.*

A number of fungi fructify in the bore-holes and brood galleries of wood- and bark-beetles, which not only disperse the spores but also introduce the fungi into the inner tissues of the host. The best-known example is the 'Dutch elm disease',† which has killed so many elms in the past thirty years. In this disease bark-beetles (chiefly *Scolytus* spp.) are responsible for the transport of the spores of the pathogen, *Ophiostoma ulmi*. The insects form characteristic 'engravings' (brood galleries) in the dead or dying elm trunks at the interface of wood and bark. The eggs are laid in the

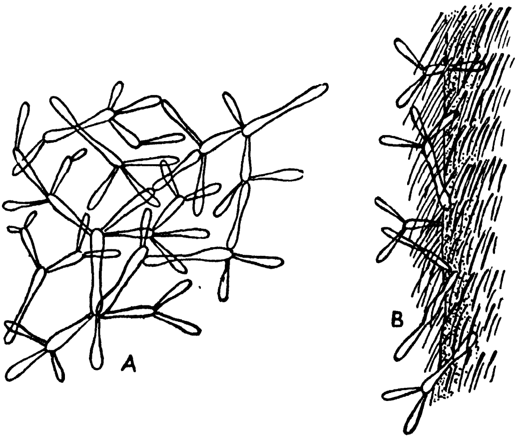

FIG. 65. *Candida reukaufii.*
A, colony of cells; *B*, groups of cells attached to the proboscis of a bee. Highly magnified, after Grüsz (1927).

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* Hautmann (1924).

† Forestry Commission (1947).

main gallery and the insects develop from egg to pupa in the lateral galleries, on the walls of which the fungus produces its heads of sticky conidia (Fig. 66).* Finally the young beetles bore their way directly outwards through the bark from the widened ends of the lateral channels, leaving little round holes in the bark so that from the outside it seems to have been peppered by shot. The emerging insects carry with them, both internally and externally, viable spores of the fungus. *Scolytus* can produce its brood galleries only in the larger limbs and trunks of dead and dying trees, but before doing so it feeds on the bark in the crutches of very small branches of healthy trees. This intro-

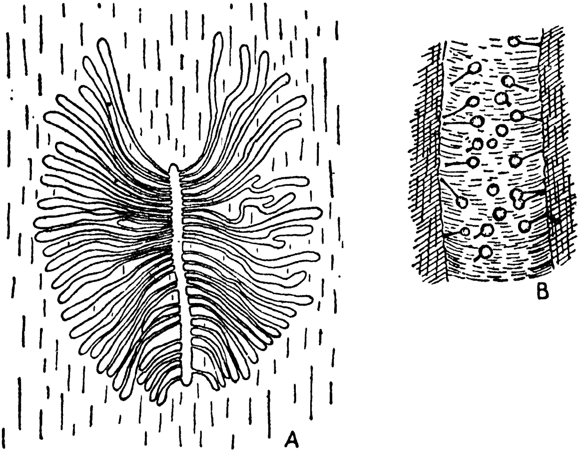

FIG. 66. Dutch elm disease.

A, brood galleries of bark-beetle (*Scolytus* sp.) at interface of wood and bark; *B*, small part of gallery magnified, showing the white heads of slimy conidia of *Ophiostoma ulmi* borne on black stalks. *A*, after McKenzie and Becker. *B* based on photographs by Clinton and McCormack.

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* The perithecial stage seems rarely to be produced in nature, but from the point of view of spore dispersal it is like the conidial stage, an extruded drop of slimy ascospores being produced at the end of a long perithecial neck.

duces the pathogenic fungus to the wood of vigorous living trees which, as they succumb in the course of years, become suitable sites for brood galleries.

The fungus *Ceratostomella ips*, which causes a 'blue stain' in the wood of conifers, has a similar dispersal story,* being spread by bark-beetles (*Ips* spp.). However, only trees already dead or very much weakened are affected because the beetles do not, as in Dutch elm disease, prepare their future victims by feeding on the younger, healthy parts before boring into the dead trunks for breeding purposes. However, the 'blue-stain' fungus, though so closely similar to the elm parasite, occurs mainly in the perithecial stage, but this is biologically just like the conidial stage of *Ophiostoma ulmi*, for a mass of slimy ascospores is borne at the end of a little stalk, but the stalk is the long neck of a perithecium the base of which is buried in the wood of the brood gallery.

The story of dispersal in the fungi (especially *Leptographium* spp.) 'cultivated' by the ambrosia beetles is somewhat similar.† The beetles bore deeply into the wood of dead and weakened trees, producing branching galleries. The fungi grow in the wood immediately surrounding the galleries and cause a characteristic darkening of the tissue. Sporulation occurs on the gallery walls and the spores are used by the grubs as food. When beetles migrate to another tree, they carry viable spores of the fungus with them and so a continual supply of 'ambrosia' is assured.

A somewhat similar association of insect and fungus is that of the fungus-growing ants.‡ These ants cultivate certain fungi in their nests in a state of more or less pure culture. When a queen establishes a new colony she

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* Leach (1940).

† Leach *et al.* (1940); Webb (1945); Bakshi (1950).

‡ Uphof (1942).

carries an inoculum of the fungus with her in her infrabucal pouch.

Again, wood wasps may enter into special relations with certain lignicolous fungi. An interesting example is the great wood wasp, *Sirex gigas*, which attacks coniferous trunks. The female has a long ovipositor.* Near the fixed end of this in the abdomen of the insect are two little pouches in which *Stereum sanguinolentum* is to be found in the oidal condition. As an egg enters the ovipositor from the main body of the insect an oidial inoculum is exuded on to it from the pouches so that as each egg is laid in a coniferous trunk the fungus is introduced at the same time. The advantage to the insect of this regular association is far from clear. Perhaps the fungus pre-digests the wood for the larva, or perhaps the larva is, in fact, mycophagous. So far as the fungus is concerned this means of dispersal, though very efficient, is merely additional to its regular spread by air-borne basidiospores.

In connexion with insect dispersal of fungi growing on tree trunks, *Cryptoporus volvatus* (Fig. 67) is of considerable interest.† It is a smallish bracket polypore, found in North America and Northern Asia on dead and dying trunks of conifers severely attacked by bark-boring beetles. When a fruit-body is about to be formed the mycelium accumulates in an old abandoned bore-hole and where this emerges the sporophore is formed. Both in general appearance and in texture it is rather like a small specimen of *Polyporus betulinus*, but the tube layer is covered in below by a firm volva. At first this is continuous, but later a small round hole is formed in it. Spores rain down from the hymenial tubes as in any other polypore, and a very small proportion of these fall through the hole and thus escape into the outer

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* Cartwright (1926); Parkin (1942).

† Hubbard (1892); Buller (unpublished).

air. The vast majority, however, are deposited on the inner surface of the volva. Through the hole in the volva, no doubt attracted by the dimness within, many insects crawl. These are mainly beetles, though not bark-beetles.

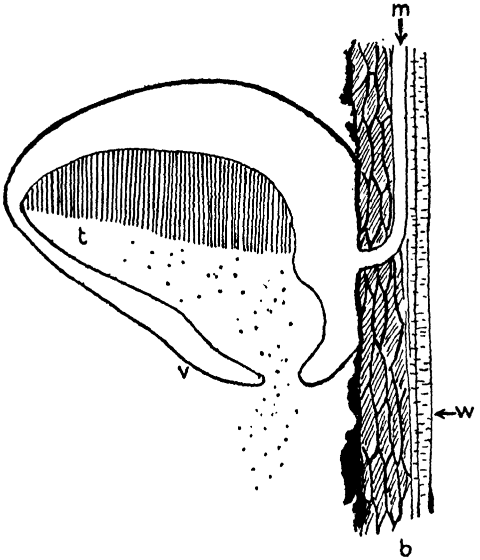

FIG. 67. *Cryptoporus volvatus.*

Vertical section of sporophore growing on a dead conifer. The sporophore is formed at the end of a mycelial strand (*m*) filling a boring made by a bark-beetle between wood (*w*) and bark (*b*). Some of the spores falling from the hymenial tubes (*t*) are seen escaping through the hole in the volva (*v*). Drawn from a half-tone figure by Henessey in Buller (unpublished).

These become contaminated with numerous spores and on emerging may go on to explore abandoned bore-holes made by bark-beetles in the trunk of another tree. So, perhaps, the fungus is dispersed, though no doubt the spores that escape directly through the hole in the volva may infect nearby trunks. The dispersal story is in need of closer study, but in view of the unique structure of the fruit-body the fungus is more likely to be entomophilous than anemophilous.

Hemipterous insects with their piercing sucking mouthparts are of great importance in the transmission of virus diseases of plants. They may also pick up the spores of certain pathogenic fungi during feeding and later introduce them into healthy plants. This type of disease is particularly found in the fruits of a wide range of species and is referred to as stigmatomycosis. The fruits are affected internally but remain sound on the outside. An example of considerable economic importance that has been much studied is the internal boll disease of cotton.* This is caused by *Ashbya gossypii* and allied fungi and leads to staining of the lint in immature, unopened bolls. The fungus grows and sporulates in the lint, but the pathogen makes no appearance at the surface of the boll. The chief vectors of the disease are bugs of the genus *Dysdercus*. When a bug feeds on a diseased boll the tip of its fine sucking apparatus punctures the ovary wall. This apparatus, throughout the greater part of its length, is sheathed in the split-tube formed by the labium, the tip of which rests on the surface of the fruit. The sucking apparatus is composed of four stylets (actually a pair of maxillae and a pair of mandibles) tightly pressed together, and contains two longitudinal tubes: a narrower one down which saliva is pumped and a slightly wider one up which the food solution is sucked (Fig. 68). The long, narrow ascospores, each with a whip-like tail, are sucked up with the liquid food and may be stored unharmed in the stylet pouches that occur in the head. Others may pass down the alimentary canal but these, apparently, soon cease to be viable. When a contaminated insect proceeds to a young and healthy boll, it

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* Fraser (1944).

may introduce the pathogen. Just how the spores pass from the stylet pouches into the host plant is not clear, but perhaps they find their way into the top of the salivary canal and are pumped thence into the host.

In a rather similar but much more casual manner, wasps may spread *Sclerotinia fructigena* amongst ripe fruit during the late summer. This 'brown-rot' organism is abundant on apples, pears, and plums, both on fruit attached to the tree and on windfalls. The rot rapidly spreads throughout an infected fruit and later, on its surface, pustules of powdery spores are formed in characteristic concentric rings. Entry is possible only through a wound and this is often provided by the bite of a wasp, which, if it has already visited a rotten fruit bearing conidia, may introduce the pathogen at the same time. This is probably the

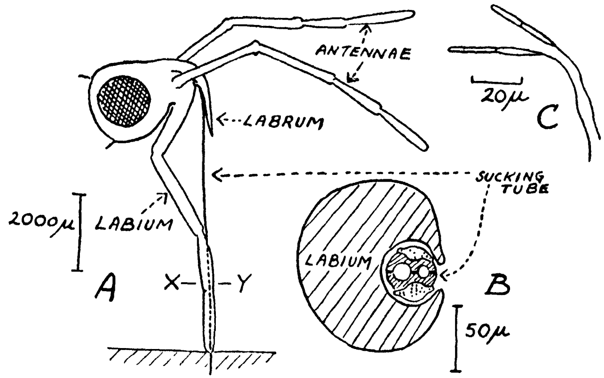

FIG. 68. *A*, head and appendages of plant bug *Dysdercus*, showing piercing-sucking apparatus puncturing the skin of a fruit; *B*, *T.S.* of labrum in region *X–Y* of *A*, showing the labium as a split tube, and the sucking tube consisting of four mouth-parts (two mandibles and two maxillae) closely set together and thus forming two tubes; *C*, spores of *Ashbya gossypii*. *A* and *B* based on figures by Fraser (1944). *C* after Ashby and Nowell (1926).

normal method by which the fungus spreads, but the spores are dry and powdery and no doubt wind dispersal occurs to some extent.

This discussion of entomophilous dispersal is by no means exhaustive and many examples have been omitted. Two points, however, stand out clearly: first, the types of insect concerned are very various (flies, beetles, moths, plant bugs, ants, bees, and wasps); second, the fungi involved are equally diverse (stink-horns, a bracket polypore, flask-fungi, smuts, rusts, yeasts, and imperfect fungi). No doubt with further work instances of insect dispersal will be multiplied, but the general statement that entomophily is rare in the fungi is likely to remain unassailed.

It should be observed that other small invertebrate animals may be responsible for the spread of fungi. Slugs,* for example, frequently feed on the larger agarics and, apparently, the spores pass uninjured through the alimentary canal and then geminate freely. Indeed, it has been claimed that slugs play a very important part in the dispersal of fleshy toadstools, but this seems unlikely. Again, mites may be effective agents in the spread of moulds. Sometimes in a mycological laboratory they become established in a few tube-cultures of moulds and then, with alarming speed, contaminants appear in nearby pure cultures. Even eel-worms may disperse fungal spores.† Thus in the *Dilophospora* disease of cereals Atanasoff claims that it is nematodes that normally carry spores to the susceptible growing-point of the shoot.

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* Voglino (1895).

† Atanasoff (1925).

V

DISPERSAL BY LARGER ANIMALS

THE larger animals may have an important part in the spread of certain fungi. Thus the dung fungi are not only dispersed by herbivorous animals, but find an ideal natural cultural medium in the faeces; some woodland subterranean fungi—truffles and their like—are, apparently, dispersed by rodents; water fowl almost certainly play an essential part in the long-distance dispersal of freshwater aquatic fungi; and finally, it is, perhaps, logical to include the activities of civilized man, who has unwittingly been responsible for the spread of many plant pathogenic fungi even from one continent to another.

When the freshly deposited dung of herbivorous animals (e.g. horse, cow, rabbit) is kept moist under a bell-jar in the light, a rich flora of fungi,* mainly minute, develops and in a fairly definite succession. Under natural conditions, in a field for example, the same flora develops but usually not in such a regular fashion, since weather changes may interfere in a drastic manner with the potential succession. Amongst Phycomycetes it is the Mucorales that provide the chief genera (*Mucor*, *Pilaria*, and *Pilobolus*) often attacked by parasites of the same order (e.g. *Piptocephalis*, *Syncephalis*, and *Chaetocladium*). The coprophilous Ascomycetes are mostly very minute forms including Discomycetes (e.g. *Ascobolus*, *Dasyobolus*, *Coprobia*, *Ascophanus*, *Saccobolus*, *Rhyparobius*, *Thelebolus*) and Pyrenomycetes (*Sordaria*, *Delitschia*, *Philocopra*, *Sporormia*, and *Chaetomium*). In Basidiomycetes the most characteristic coprophilous genus is *Coprinus*, many species being restricted to dung. Most of

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* Massee and Salmon (1901).

these fimicolous *Coprinus* spp. are small and in the latest stages in the development of the dung flora there is often a forest of tiny fruit-bodies. Further, conidial fungi are commonly to be seen. These may be 'imperfect' stages of Ascomycetes* or Basidiomycetes, but a number of Fungi Imperfecti also occur. One of the commonest of these is *Arthobotrys oligospora* which catches and consumes the eel-worms that may occur in vast numbers in the dung.

In the development of this coprophilous flora there tends to be a succession. Phycomycetes come first, followed by Ascomycetes, leading to a final stage dominated by Basidiomycetes (*Coprinus* spp.). The phases, indeed, overlap, but the story of succession is usually fairly definite. However, there has been no careful study of the causes of this succession. Very probably the early appearance of the mucoraceous fungi is due to the rapidity with which they grow and sporulate, and the delay in development of agarics to relatively slow growth of the mycelium and the late stage at which sporophores are differentiated.

The general story of dispersal in most of the dung fungi would seem to be the same. The spores produced by the sporophores on the dung reach the surrounding grass, which may later be eaten by a horse, cow, or rabbit. The spores not only pass uninjured through the alimentary canal of the animal, but encounter there conditions stimulating germination,† which takes place usually in the deposited dung. The spores of some coprophilous species will germinate only if treated to some of the conditions encountered in the intestine, such as a relatively high temperature, or an alkaline reaction, or both. However, some species can germinate without any such treatment. Spores of the dung *Coprini* need no special conditions, and, although the germination of *Pilobolus* spores is greatly stimulated by a

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* Barnes (1924).

† Gwynne-Vaughan and Barnes (1935).

high temperature, a small percentage do germinate under ordinary conditions.* Since the spores of some fimicolous fungi can germinate in nature without passage through an animal, it is clear that some of the species that make their appearance on dung may develop from air-borne or insect-borne spores, but there is little doubt that the normal channel for dispersal is through the animal.

So far as their apparatus of dispersal is concerned, some of the dung fungi seem little, if at all, modified in connexion with their peculiar habitat. Little or no specialization is to be seen in the coprophilous species of *Mucor*, *Coprobia*, *Chaetomium*, or *Coprinus*, but, on the other hand, species such as *Pilobolus* spp., *Dasyobolus immersus*, *Saccobolus* spp., and *Sordaria* spp. show, in the organization of their spore discharge, beautiful and parallel adaptation. This specialization is associated with the first stage of dispersal—the passage of spores from the dung to the grass. In these fungi the spores are discharged to such a distance (10–200 cm.) that they can reach the grass without the aid of wind. The distance (d) to which a microscopic spherical projectile is shot when discharged with a given initial velocity is given by: $d = Kr^2$ where K is a constant depending on the physical characters of the air and r is the radius of the projectile. The long range of the spore-guns of specialized coprophilous fungi is due rather to the comparatively large size of the projectile than to a greater muzzle velocity. For such minute bodies as spores the resistance of the air is the principal factor limiting the height or distance of discharge, and the smaller the projectile the more serious is this factor. In some of the specialized coprophilous fungi the individual spores are small, but they are bound together by mucilage to form projectiles of larger size. This is so in *Pilobolus* spp. in which the whole sporangium, containing hundreds or

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* Buller (1934).

thousands of spores, forms the projectile; in the minute discomycete *Thelebolus nanus*, where the ascus-contents of 200–300 spores are all cemented together by slime; and in the pyrenomycete *Sordaria curvicolla* in which the spore-mass discharged from the ascus consists of 128 spores bound together. In some other species, notably *Dasyobolus immersus* and *Sordaria fimiseda*, the eight spores of the ascus are not only stuck together by mucilage but also are relatively enormous (Fig. 69).

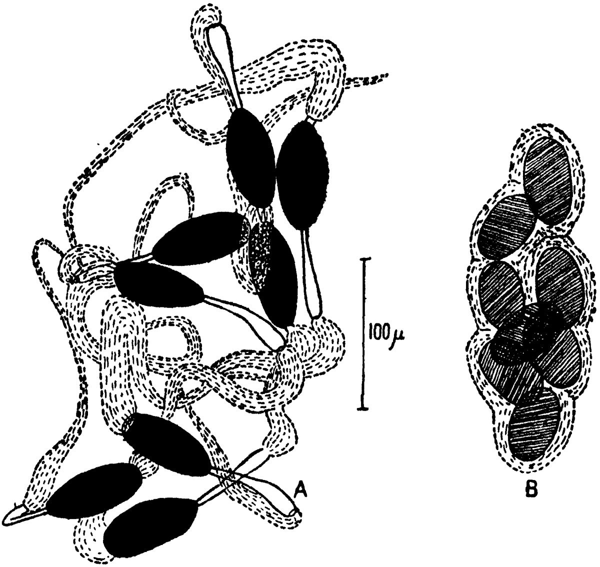

FIG. 69. Group of ascospores discharged from an ascus of *Sordaria fimiseda* (*A*) and from an ascus of *Dasyobolus immersus* (*B*).

In some of the more specialized fungi growing on the dung of herbivores the parallel evolution of spore-discharge equipment is outstanding. This may be best emphasized by considering the three common types: *Pilobolus*, *Dasyo-*

bolus immersus, and *Sordaria* sp.* In all the spore-projectile is relatively large, the spores being held together by mucilage. In all the distance of discharge is considerable: up to 200 cm. in *Pilobolus*,† about 60 cm. in *Dasyobolus immersus*,‡ and some 25 cm. in *Sordaria curvula*.§ These distances of

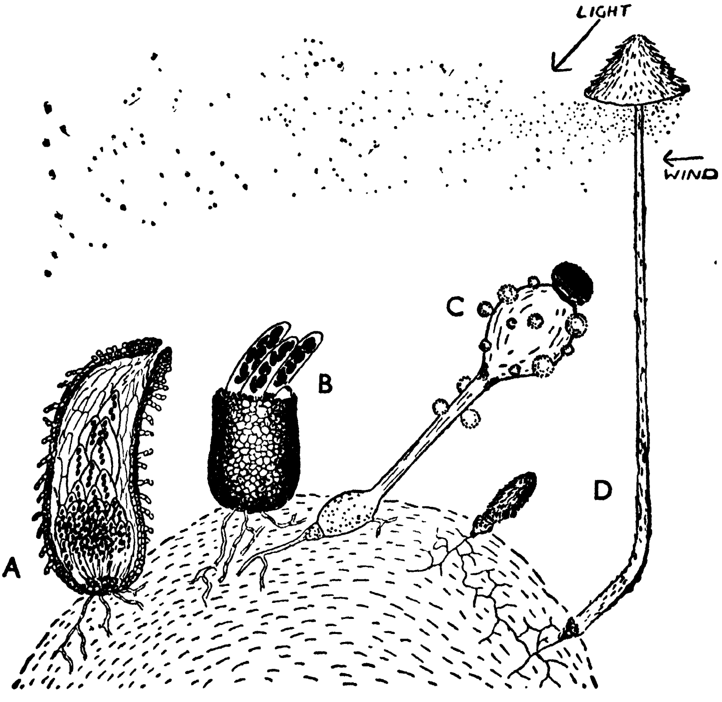

FIG. 70. Diagram showing reaction to light of some coprophilous fungi.

A, *Sordaria tetraspora* (seen in optical section), × 50. *B*, *Dasyobolus immersus*, × 40. *C*, *Pilobolus kleinii*, × 10. *D*, *Coprinus fimetarius*: left, young sporophore primordium orientated by positive phototropism; right, mature expanded fruit-body liberating spores, nat. size.

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* e.g. *Sordaria curvula*, *S. minuta*, *S. tetraspora*, and *S. fimiseda*, species formerly included in the genus *Podospora*.

† Buller (1934). ‡ Buller (1909). § Ingold (1933).

discharge are sufficient to carry the spores on to the surrounding grass without the aid of wind. In all discharge is by day and the spore gun is orientated by the phototropism of the sporangiophore in *Pilobolus*, the individual projecting asci in *Dasyobolus*, and the perithecium neck in *Sordaria*. This positive phototropism helps to ensure that the spore projectile shall be thrown clear of the substratum. In all the projectile is strongly adhesive, the mucilage cementing it firmly to the stems and leaves of the surrounding herbage. There is some evidence that light has an injurious effect on fungal spores, and it is therefore of interest to notice in these three fungi that in the spore-masses discharged on to the grass the protoplasm is shaded by the pigment of the spore-wall in *Dasyobolus* and *Sordaria* and by the black part of the sporangial wall in *Pilobolus* which effectively covers up the discharged mass of almost colourless spores cemented to a blade of grass.

A strong case* can be made for adding *Sphaerobolus stellatus* to the list of highly specialized coprophilous fungi, although in Britain this common fungus is much more familiar as a lignicolous species. There is no doubt, however, that it may at times be coprophilous, and then its dispersal story is exactly like that of *Pilobolus*.† It has nearly all the features of the specialized coprophilous species, with its large, adhesive spore-mass (peridiolum) projected to a considerable distance (5 metres) and aimed towards the incident light by the phototropism of the sporophore. Discharge is diurnal and the spores and gemmae in the projected peridiolum are screened from light by a thin, brown membrane. Another gasteromycete that belongs to the coprophilous flora is *Cyathus stercoreus*, fairly common on

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* Buller (1934).

† Possibly the forms growing on cow-dung should be regarded as separate species (see Parker-Rhodes (1951)).

old manure in North America. The blackish, egg-like peridiola within the 'splash-cup' of the open fruit-body are scattered by rain on to the surrounding grass, where each sticks firmly by means of its gelatinous funiculus. No doubt the peridiola are eaten with the grass and the same cycle occurs as in most coprophilous species.

It must again be emphasized that by no means all the dung-fungi show a high degree of structural specialization in relation to their peculiar environment. In species of *Ascophanus* and *Coprobia* the spores are colourless and are not glued together in the ascus to form a single mass, but are discharged so that they separate in the air, as in most non-coprophilous Ascomycetes. In consequence, the distance of discharge is only a few centimetres and they rely on wind to carry the spores to the nearby grass. *Thelebolus nanus* (Fig. 71) is an interesting example of a partially specialized form. This normally produces only one ascus at a time (probably daily for a few days) but it contains approximately 256 (i.e. 2^8) spores. These are bound together in a single spore-mass and are discharged to a height of about 7 cm. However, the spores are quite hyaline and unprotected from strong light.

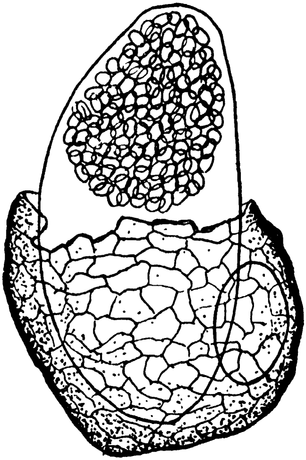

FIG. 71. *Thelebolus nanus*. Apothecium with one ripe ascus partially protruding and one very young ascus seen through the wall of the apothecium. × 525.

Again, in the coprophilous agarics specialization, if it may be said to exist, is very slight. The spores are liberated as in other gill-bearing fungi and wind is responsible for dispersal to the surrounding grass. It is, however, interesting to notice that coprophilous agarics have black (*Coprinus*, *Anellaria*, *Panaeolus*) or dark-brown (*Stropharia semiglobata*) spores, so that again the protoplasm is protected from light during the sojourn of the spores on the grass before it is eaten. Although black-spored agarics are by no means limited to the dung habitat, it seems unlikely that the regularity with which black or near-black spores are associated with coprophilous species is a matter of pure chance.

Just how the spores of the coprophilous Mucorales (especially *Mucor* spp. and *Pilaria anomala*) reach the grass from the dung is not clear. It has already been noted that most species of *Mucor* form sporangial drops. A projectile of *Pilobolus* might, immediately after discharge, brush against such a drop, picking up some spores which might then be carried as passengers to the surrounding herbage. That this does happen can easily be demonstrated by catching *Pilobolus* sporangia in mid-air on the surface of sterile nutrient agar, when a growth of *Mucor* frequently develops from the projectile, but this seems improbable as the main method of primary dispersal; perhaps splashing rain or insects play a part.

On the excreta of frogs a minute phycomycete, *Basidiobolus ranarum** occurs with great regularity. It seems to be on its own and no coprophilous *flora* develops as on the dung of herbivores. Interest centres on the fact that the fungus is so like a tiny *Pilobolus* although, systematically, there is a considerable gulf between them. How the conidium is discharged to a distance of several centimetres has already been discussed. But this is not the end of the story of dispersal. Small beetles feed on the discharged spores, but before the spores have lost their viability the insects

* Levisohn (1927).

may be devoured by a frog. In its intestine the conidium, which is really an immature sporangium, completes its development and gives rise to eight sporangiospores. These are voided with the excreta and germinate to give mycelia there.

The hypogeal fungi form an interesting biological group. The fruit-bodies, varying from a few millimetres to several centimetres in diameter, are buried in the soil beneath the leaf carpet in woods. In most of them the story of dispersal would seem to be the same, but observations are few and experimental work is apparently completely lacking. In a number of these fungi the fruit-body gives off a smell which attracts rodents. These grub up the fruit-bodies and eat them. The spores no doubt pass through the alimentary canal and are distributed in the droppings. But these fungi are not coprophilous. They are soil fungi but some, perhaps all, enter into mycorrhizal relations with forest trees.

In hypogeal fungi convergent evolution has clearly occurred, the same type of fruit-body having evolved in Endogonaceae (a family of Mucorales), in Hymenogastraceae (a family of Basidiomycetes) and in two very distinct families of Ascomycetes (Elaphomycetaceae and Tuberaceae). Even in Tuberaceae there does not appear to have been a single line of evolution. Apparently the hypogeal types included in this family have arisen in three rather distinct ways from epigeal forerunners.

Perhaps the commonest British hypogeal fungus is *Elaphomyces granulatus* (hart's truffle) occurring both in deciduous and coniferous woods. Often the little excavations where rodents have grubbed for the fruit-bodies are to be seen* and sometimes an abandoned half-nibbled specimen may be discovered left behind, no doubt, when the animal was disturbed. It is well known that the French,

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* Hastings and Mottram (1915).

much more inclined to mycophagy than the British, train dogs and pigs to locate truffles, but which animals are mainly responsible for dispersal in nature does not seem to have been studied. Studies on the germination of the spores of these fungi might yield interesting results.

FIG. 72. Mycologists raking for truffles during a fungus foray at Hereford. Reproduced from a small panel of a full-page illustration by Worthington Smith in the *Graphic* of 1873.

Hypogeal fungi are usually regarded as rather rare, but this is only because few have taken the trouble to look for them. In Britain many records were made last century largely due to the activities of Broome who, armed with a hand-rake, searched methodically for these fungi (Fig. 72). In very recent years this practice has been revived by Dr.

L. E. Hawker and her students. On the foray of the British Mycological Society at Bangor, North Wales, in 1950 an hour's raking by half a dozen members under Dr. Hawker's leadership brought to light under a single tree six different species of hypogeal fungi divided amongst Phycomycetes, Ascomycetes, and Basidiomycetes.

There is probably a certain amount of casual dispersal of resistant fungal spores which are able to pass uninjured through the alimentary canal of larger animals. Sometimes dispersal of this kind may be of some importance. An example is *Plasmodiophora brassicae*, causing club-root of crucifers. If diseased turnips are fed to cattle, the minute resting spores get into the dung. If this is used as manure viable spores are added to the soil and may cause infection in a cruciferous crop. For this reason many gardeners prefer to use artificial fertilizers rather than run the risk of introducing this fungus by the use of natural manure.

Birds have occasionally been suspected of transporting fungal spores and there is some evidence that they may have played a part in the disastrous spread of the bark disease of American chestnut in the second decade of this century. Plant pathologists in the United States made a thorough study of the dispersal of the causal organism *Endothia parasitica*. The local spread of the disease from tree to tree in a single wood was clearly due to air-borne ascospores discharged from perithecia during wet weather, but it was thought that the occasional long-distance dispersal to remote plantations might be due to ascospores or pycnidiospores carried by birds, especially woodpeckers and tree creepers, on their breasts, tail feathers, feet, and beaks.* Birds were shot in the neighbourhood of infected trees and a 'poured plate' technique was used in estimating the spore load on each bird. Two downy woodpeckers

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* Heald and Studhalter (1914).

were each found to be carrying over half a million and a brown tree creeper over a quarter of a million viable spores. The general conclusion was reached that many of the local centres of infection isolated from the general area of chestnut bark disease might well have originated from spores carried by these birds.

No doubt water fowl are concerned in the dispersal of freshwater aquatic fungi. In spite of the fact that these fungi have no air-borne spores, the distribution of individual species is just as wide, if not wider, than that of terrestrial species. This raises the problem of the dispersal of these fungi from one isolated freshwater system to another, and there can be little doubt, in spite of the absence of direct evidence, that, as with other aquatic plants, water birds play an essential part in their long-distance dispersal.

It would be long and rather tedious to discuss in detail the influence of Man on the dispersal of fungi. Occasionally he deliberately aids in dispersal such as when he distributes mushroom 'spawn' or cultures of moulds for the manufacture of cheese, but usually dispersal is an incidental concomitant of his global activities from which he may suffer considerably. It is in the intercontinental spread of pathogenic fungi that Man's influence has been most marked.

Such vast expanses as the Atlantic and Pacific Oceans appear to offer formidable or perhaps insuperable barriers to the spread of fungal spores. But where Nature has failed Man has unwittingly succeeded. The story of plant pathology in Britain is punctuated by invasions from the Western Hemisphere, e.g. potato blight (introduced about 1840) and American gooseberry mildew (about 1900). And the North American Continent has received its share of pathogens from Europe such as the blister rust (*Cronartium ribicola*) of white pine (introduced about 1906) and Dutch elm disease (about 1930). Further at least one serious disease in North America, the bark disease of chestnut, appears to have originated in China or Japan.

The spread of fungal diseases from one continent to another has, apparently, been due largely to the introduction of infected material (e.g. nursery stock) of the host plant rather than to the accidental transport of individual fungal spores. Through bitter experience Man has now learnt that great care must be taken to prevent the spread of disease-producing fungi to new areas, and in most countries has taken steps, often fairly effectively, to guard against the introduction of further pathogenic species from abroad.*

* Butler (1917); Stakman (1947).

VI

SEED-BORNE FUNGI

A NUMBER of fungi are dispersed in an association of some kind with the dispersal units of the host. These units are usually seeds, or seed-like fruits such as the caryopses of cereals or the mericarps of umbellifers. Although seed-borne fungi have but a small place in the general picture of fungal dispersal, they are of great significance to the plant pathologist since many important plant diseases are seed-borne.*

There are a number of endophytic fungi, causing systemic infections of their hosts, that are normally seed-dispersed and, at least under natural conditions, do not seem to be dispersed in any other way. Thus in members of Cistaceae an endophytic fungus is regularly present. The story has been studied in some detail in *Helianthemum chamaecistus*.† The fungus is found in root and shoot, and when flowers are produced enters the ovary wall. The outer gelatinous coat of the testa is infected, but the fungus is prevented by a barrier of tannin-filled cells from passing into the embryo and endosperm. Infection of the seedling from the dormant mycelium in the testa occurs at germination and under natural conditions for continued growth such infection seem to be necessary. Much earlier work by Rayner‡ on the endophytic mycorrhiza of *Calluna vulgaris* and other ericads gave a picture essentially like that in *Helianthemum*. However, workers on ericaceous mycorrhiza have reached conflicting conclusions. There is no certainty that infection of *Calluna* is systemic nor that the *Phoma* isolated from the seeds is responsible for the mycorrhizal

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* Orton (1931); Muskett (1950).

† Boursnell (1950).

‡ Rayner (1915).

roots. All is obscure and the whole subject is in need of critical re-investigation.*

Another fungus that apparently relies entirely on seed dispersal is the well-known endophyte of *Lolium* spp.† which does not seem to be a symbiont but merely a harmless parasite. The fungus forms an intercellular mycelium throughout the shoot system of the host. In due course the ovary is infected and the caryopsis carries a dormant mycelium in the testa (Fig. 73). With some difficulty the fungus has been isolated in pure culture, but no spores were produced so, as with the endophyte of *Helianthemum*, its systematic position is unknown. From *Lolium* a second

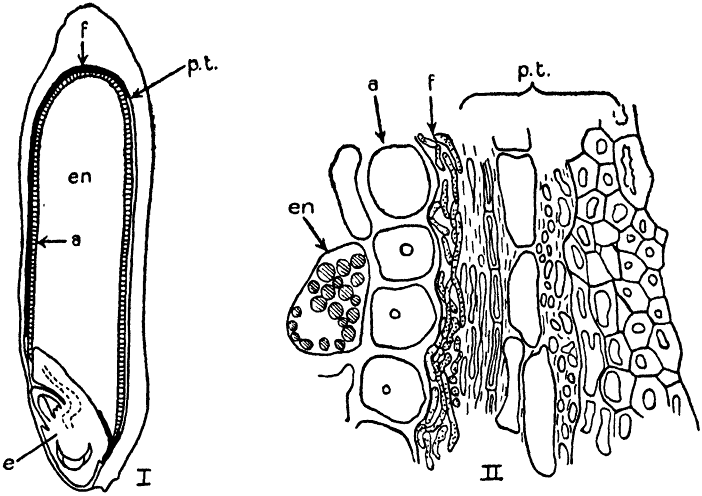

FIG. 73. I, *L.S.* grain of *Lolium*, and II, small part much more highly magnified. *e*, embryo; *en*, starchy endosperm; *a*, aleurone layer; *p.t.*, fused pericarp and testa; *f*, layer of hyphae of endophytic fungus. After Freeman (1904).

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* Harley (1950).

† Freeman (1904).

endophyte can sometimes be isolated which grows well in culture and produces microconidia. Although most specimens of *Lolium* are infected some are free from either endophyte. On making reciprocal crosses between infected and uninfected plants it has been shown that the fungus is 'inherited' only through the ovule.*

Another interesting fungus that is sometimes seed-borne is *Epichloe typhina*, the 'choke' of grasses. This attacks a number of species belonging to several genera causing systemic infection. In *Dactylis glomerata* flowering is prevented in affected plants and the disease cannot, therefore, be seed-borne. However, when *Festuca rubra* is attacked† it still produces seed and these may carry the fungus as a resting mycelium in the embryo and endosperm. Further, plants of *F. rubra* may show no external manifestations of disease, no stroma being formed. Where this type of latent infection occurs the fungus is dispersed solely with the seed of the host and a condition of affairs very like that of *Lolium* and its endophyte is attained.

Amongst important plant diseases that are normally seed-borne, the smuts of cereals are outstanding. Most smuts are systemic with the fine intercellular mycelium extending throughout the host plant. Spore production, however, is usually localized in and about the reproductive organs. In cereal smuts the ovary is the chief centre of spore production and no good grains are formed by infected plants, but instead of the grain there is formed a covered or uncovered mass of blackish brand spores. In stinking smut (bunt) of wheat caused by *Tilletia caries*, the wall of the caryopsis is unaffected but the interior is filled with black spores smelling of decaying fish due to the production of trimethylamine. During harvesting these grains are broken and the brand spores get dusted over healthy grains

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* Sampson (1935, 1937, 1939).

† Sampson (1933).

where they remain dormant until sowing time. The grains of wheat and the brand spores germinate at the same time and so infection of the seedlings is assured. Here the fungus is carried merely on the surface, so that the disease is easily controlled by shaking the grain in a drum with an organo-mercurial dust. It is of interest that, although this fungus is normally seed-borne, it is not necessarily so. Thus where an infected crop is threshed on the spot, spores may settle on the nearby soil, remain dormant but viable, and infect clean seed sown in the following season.

In *Ustilago nuda*, the loose smut of wheat and barley, the story is rather different. Spikelets of diseased plants are reduced to an exposed mass of brownish-black brand spores at a time when the uninfected plants are in flower. The dry powdery brand spores are wind borne and may reach the stigmas of healthy plants, but instead of being resting-spores they germinate at once to produce a mycelium which penetrates the ovary and enters the developing seed. The seeds, however, are not destroyed but simply contain the fungus in a resting condition, so that at germination the seedlings are already infected. In such smuts surface sterilization of the grain is useless and control depends on the fact that the fungus is more sensitive to heat than the embryo of the seed, so that steeping in hot (50–52° C.) water for a short time (about fifteen minutes) kills the parasite without greatly affecting the viability of the grain.

Another group of cereal diseases that are typically seed-borne are the 'stripe diseases' caused by *Helminthosporium* spp. *H. avenae* is responsible for leaf stripe and seedling blight of oats.* Except for a very local spread of the disease due to air-borne conidia during the growth of the crop, dispersal is dependent on infected grains which have a

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* Turner and Millard (1931).

resting mycelium on their surface and may also carry viable conidia, although their importance is relatively slight. *H. gramineum*, causing leaf stripe of barley, is similar, but the resting mycelium is usually in the grain between pericarp and testa.

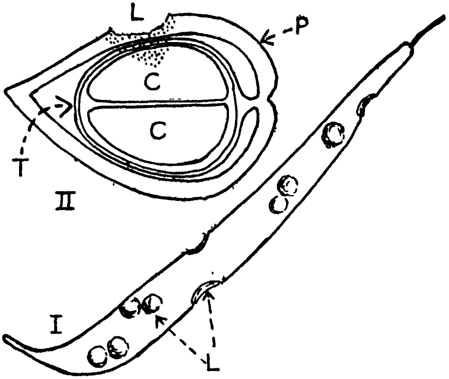

FIG. 74. Runner bean attacked by *Colletotrichum lindemuthianum.*

I, diseased pod; II, *T.S.* diseased pod and contained seed with region invaded by fungal hyphae indicated by dotting; *L*, lesions caused by the parasite; *P*, fruit wall; *T*, testa of seed; *C*, cotyledons of embryo. After Whetzel.

Seed-borne fungi are specially prominent in the Gramineae, but they are also common in other families of flowering plants. Some of the diseases of pulses are seed-borne. A well-known example is anthracnose of french and runner beans due to *Colletotrichum lindemuthianum*. On all parts of the shoot this fungus produces small circular lesions in association with which slimy conidia are formed and are dispersed locally by rain-splash. Where the pods are infected the parasite may spread to the developing seed which ripen with the fungus deeply situated in the tissue of the cotyledons (Fig. 74). The appearance of disease in the following season is due almost entirely to the use of infected seed. The fungus is too far embedded in the embryo for seed sterilization to be effective, and control consists largely in the use of clean seed. The story of leaf, stem, and pod spot of peas caused by *Ascochyta pisi* is very similar.

Flax is of special interest because its principal fungal diseases are seed-borne.* Thus seedling blight caused by *Colletotrichum linicola* is carried over from one season to the next as a resting mycelium in the outer layers of the seed-coat. Stem break and browning due to *Polyspora lini* is transmitted in much the same manner, and this is also true of the grey mould (*Botrytis cinerea*) which may hibernate as a resting mycelium in the outer layers of the testa. However, *B. cinerea* is a very unspecialized and common parasite occurring on a large range of hosts and also as a saprophyte on dead plant material, but the early infection of the flax seedlings is commonly from the seed-borne mycelium, and only in connexion with later infections are other sources of inoculum important. Other flax diseases such as foot rot, due to *Phoma* spp., and wilt, caused by *Fusarium lini*, may also be seed-borne, but infection of the new crop is often directly from the soil. In Northern Ireland, a great flax-growing centre, the examination of flax seed for the presence of seed-borne fungi has become an important aspect of seed-testing. In the method used (Ulster method) a random selection of seeds from a sample is placed on sterile malt agar in petri dishes. These are incubated at 22° C. and examined five days later. If a seed carries one of the important flax pathogens that are capable of rapid growth on agar (e.g. *Colletotrichum linicola*, *Polyspora lini*, *Phoma* sp., *Botrytis cinerea*, and *Fusarium lini*), a characteristic colony develops on the medium around the

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* Muskett and Colhoun (1947).

seedling (Plate VIII). Although the seeds may carry surface spores of saprophytic moulds (especially *Penicillium* spp.), their growth does not, in practice, interfere with this simple and effective test, which can be carried out on a large scale and gives a clear picture of the degree to which the seed is contaminated and of the nature of the pathogens present. In Holland also examination of seed samples of crop plants for the presence of parasitic fungi has become an important part of seed-testing.*

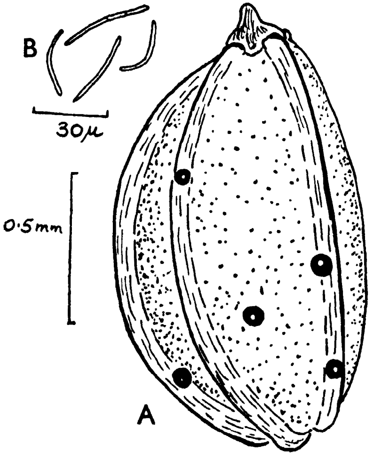

FIG. 75. *A,* celery 'seed' (mericarp) infected with *Septoria apii.* Five pycnidia showing. *B,* spores liberated from the pycnidium on moistening the 'seed'.

So far examples have been considered where the fungus is seed-borne as a resting mycelium or as spores or both, but sometimes a whole fruiting structure is involved. This is so in *Septoria apii,* which causes leaf-spot of celery (Fig. 75). All parts of the shoot may be affected, causing

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* Doyer (1948).

local infection-spots bearing pycnidia. From these, long pycnidiospores ooze out embedded in slime and may be splash-dispersed. The developing fruits are often infected and on the mature mericarps ('seeds') pycnidia are frequently formed. These remain alive but dormant when the 'seeds' are dry, but when they are soaked and germination occurs, spores ooze out from the pycnidia and infect the seedlings.

Apart from those diseases in which the fungus is actually carried in some way or other on or in the viable seed, there are a number of fungal diseases where the pathogen, though not actually attached to the living seed, tends to be dispersed as a contaminant of the seed sample. This type of dispersal is somewhat unnatural, but may be of considerable economic importance. For example, a sample of rye seed may contain sclerotia of ergot (*Claviceps purpurea*), and at sowing-time these are scattered with the grain. Again, in the blind-seed disease of *Lolium* spp.* caused by *Phialea temulenta*, infected seeds are not viable, but in a commercial sample may be mixed with healthy ones. Both types are sown together and the 'blind' seeds may give rise to apothecia from which ascospores are discharged, infecting the ovaries of rye-grass and darnel and thus leading to the formation of more 'blind' seeds. Even some rust fungi may be 'seed-borne' by being included in a commercial seed sample. When seed from a rusted flax crop is harvested teleutospores of *Melampsora lini* attached to small fragments of fruit-walls and leaves get mixed with the seed.† Next season these fragments are scattered with the seed and in due course the teleutospores germinate to produce basidiospores which are discharged and infect the young flax plants.

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* Wilson, Noble, and Gray (1945).

† Muskett and Colhoun (1947).

The various types of seed-borne fungi have been illustrated by reference to a few scattered examples, but there are very many more, and plant pathologists are becoming increasingly aware of the importance of this type of dispersal in agricultural practice. How far seed dispersal is of importance for fungal pathogens attacking plants under natural conditions is not yet known. Harley* reports the examination of seeds of a number of wild and garden plants removed with due precautions from unopened capsules and left overnight in sterile water. He says: 'Excluding Cistaceae and Ericiceae, in all of which fungi occurred, eleven out of twenty-five species were seen to bear hyphae on some of the seeds.'

A consideration of seed-borne fungi shows all types of association, from the most casual one in which the spores simply adhere to the surface of the grain (e.g. *Tilletia caries*) to the most highly organized where the fungus has ceased to sporulate and relies entirely for its dispersal on a seed-borne mycelium (e.g. the endophyte of *Lolium*).

From the point of view of disease prevention the location of the parasite in the seed is of great importance. Surface infection, with the spores or resting mycelium on or near the surface of the seed or seed-like fruit, is the commonest type and can usually be tackled successfully by seed treatment with a suitable fungicide. However, where deeper tissues are affected disinfection cannot be achieved in this way. Luckily, deep-seated infection is rarer. In *Ustilago nuda*, as already mentioned, seed sterilization can be effected by hot-water treatment, but this is not a method of general application. In anthracnose of beans, for example, the only efficient method of control is to avoid the use of seed from a diseased crop.

The types of fungi that are normally seed-borne, in the

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* Harley (1950).

sense that the fungus is actually in or on the seed, are rather limited. Amongst Basidiomycetes they are smuts. Otherwise they are mostly Fungi Imperfecti or Ascomycetes in the 'imperfect' stage. The main groups of truly obligate parasites (i.e. Peronosporaceae, Erysiphales, and Uredinales) are not usually seed-borne. It is interesting to note that in all these there is not only a well-developed air-borne stage, but also an efficient hibernating stage. Seed-borne infection as often as not serves rather as a method of hibernation than of dispersal.

The plant pathologist often extends the conception of seed-borne fungi to include those carried by vegetative reproductive units or 'planting units' such as tubers, bulbs, and runners.* But although dispersal of this nature may be of great practical significance, it has little importance in nature, and comes under the heading of 'Man as an agent in the spread of fungi'.

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* Muskett (1950).

VII

WATER AND THE DISPERSAL OF SPORES

IT is necessary to distinguish between the part played by water in the dispersal of terrestrial fungi and the state of affairs encountered in the true aquatic fungi, where water is the medium in which the spores are dispersed.

In the development of all land fungi water is a factor of utmost importance, and without an adequate supply growth and sporulation are impossible. Again, in those fungi in which the spores are violently discharged, spore liberation can occur only whilst the cells of the hymenium remain turgid, and the supply of water to maintain this turgidity is vital for spore liberation.

However, in land fungi water may play a more direct part in dispersal and the kinetic energy of moving water may be used in scattering the spores. This is probably so in a large number of slime-spore fungi. For example, *Colletotrichum lindemuthianum*, the cause of anthracnose in dwarf and runner beans, produces its spores on the pods in pink, slimy masses. Heavy rain falling on the diseased pods may bespatter the neighbouring healthy pods with spores of the pathogen and so spread infection. Another example, to which reference has already been made, is the conidial (*Fusicladium*) stage of apple scab (*Venturia inaequalis*). Although they are 'dry-spores', the conidia are too firmly attached to their conidiophores to be liberated by the wind alone, but separate easily when wetted and are apparently normally dispersed by wind-driven rain. Again, in the puffballs (*Lycoperdon* spp. and *Geaster* spp.) heavy rain, or large drops of water dripping from the foliage of trees, may bring about the liberation of visible puffs of spores (Fig. 76). A large drop striking the dry, papery, unwettable peridium, locally and momentarily depresses it, with the result that the fungus behaves like bellows and there issues a puff of spore-laden air—a puff bearing millions of spores.*

In all these examples the relation of rain-splash to dispersal is somewhat casual and it can hardly be said that the fungal structure has become modified in connexion with splash dispersal. However, in the bird's-nest fungi (*Cyathus* spp. and *Crucibulum vulgare*) there is a strong suggestion that the open fruit-body with its contained peridiola has a special survival value as a 'splash-cup'† (Fig. 77). Drops of water falling from a height into the open fruit-body are broken up and reflected from the interior of the splash-cup, often carrying peridiola with them to a distance of several yards (Fig. 78). This method of dispersal can easily be demonstrated by allowing drops of water to fall from a height into an open fruit-body of *Crucibulum vulgare* or *Cyathus* spp. A peridiolum striking an object becomes firmly attached because of the sticky nature of its funiculus.

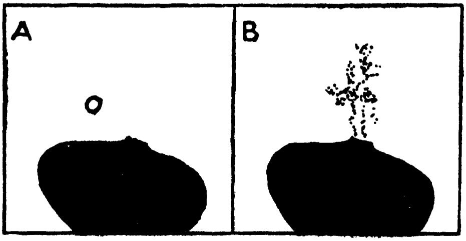

FIG. 76. *Lycoperdon perlatum.*

A, falling drop (5·0 mm. dia., speed 440 cm./sec.) 0·0017 sec. before striking peridium; *B*, 0·046 sec. after impact—a cloud of spores is issuing through ostiole. Copied from stills (see Gregory (1949)) of an ultra-high-speed film.

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* Gregory (1949).

† Brodie (1951).

In the field, around fruit-bodies of *Cyathus striatus*, the bird's-nest fungus with the most specialized splash-cup, dispersed peridiola can often be seen hanging by the funiculus from nearby leaves. Splash-cups are not limited to these fungi, for the same mechanism has arisen in the liverwort *Marchantia polymorpha*, where the gemma-cups are essentially similar, and perhaps also the soredia-lined podetia of the lichen *Cladonia pyxidata* may be interpreted in the same way.

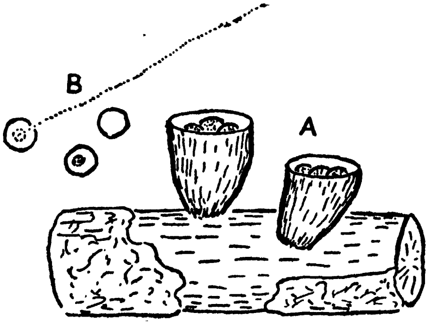

FIG. 77. *Crucibulum vulgare.*

A, two fruit-bodies on a partially decorticated twig; *B*, three peridiola, in one of which the slimy funiculus is shown extended.

Trickling rain-water may also play a small part in the spread of some fungi. In the American chestnut bark disease caused by *Endothia parasitica*, spread of infection from tree to tree is usually due to ascospores violently discharged into the air. However, in addition, the fungus produces pycnidiospores which ooze from the pycnidia in slimy masses and are spread by rain trickling over the surface of the trunk, perhaps causing further infections in the same tree.

Again, rain percolating through the soil may be of importance in the dispersal of some species. In *Phytophthora infestans* the conidia produced on the leaves of diseased plants may fall on to the soil below and be washed down by rain to infect the potatoes below. As the water percolates downwards, spores will tend to be stranded on soil particles and on organic debris. Consequently tuber infection can be much reduced by thorough 'earthing up' of the plants, so that spores are more likely to be filtered out of suspension before the rain-water reaches the tubers.

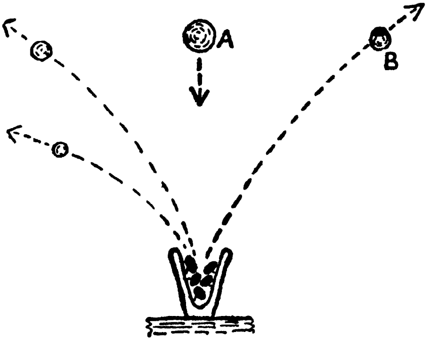

FIG. 78. Diagram of splash-cup in *Crucibulum* at the moment when a drop (*A*) is about to fall into it, and also the supposed appearance a minute fraction of a second later when the fallen drop has been broken up and reflected from the cup, one of the resultant droplets (*B*) carrying a peridiolum with it.

The downward movement of fungal spores in a sandy soil has been studied experimentally* and it has been found that whilst wettable slime-spores such as those of *Zygorrhyncus vuillemini* and *Gliomastix convoluta* are readily washed down through the soil, the spores of *Penicillium* sp., which have non-wettable coats, remain at the surface and are not carried down by percolating water. In conformity

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* Burges (1950).

with this result it appears that the fungi isolated from the lower layers of soil tend to have slime-spores, whilst species isolated at or near the soil surface tend to be dry-spored.

Apart from its actual surface the soil is a more or less aquatic environment, and it therefore causes no surprise to find some true water moulds (e.g. *Achlya* spp., *Saprolegnia* spp., and certain chytrids) as normal members of its fungus flora.

There are a number of fungi which, while themselves essentially terrestrial, grow on waterside or reed-swamp species of higher plants. Reproductive units of these fungi may be dispersed on the surface of the water. For example, in *Sclerotinia scirpicola*,* a parasite of *Scirpus lacustris*, the sclerotia formed in the old stalks are liberated into the water when these break up, and are later to be seen floating on the surface and stranded on the shores of lakes. Floating and stranded sclerotia produce aerial apothecia in the Spring, from which discharged spores are air-borne to their hosts.

In the completely aquatic fungi the spores are produced, liberated, and normally dispersed below water. Fungi are predominantly land organisms with between 50,000 and 100,000 'good' species so far described, but of these only about 2 per cent. are aquatic. In the majority of aquatic fungi the whole evolutionary story seems to have been in water and they are branded as primitive aquatics by the possession of zoospores. On the other hand, there are a number of submerged aquatic Ascomycetes and Fungi Imperfecti which appear to have migrated from land to water. No basidiomycete is known to have taken this seemingly retrograde step.

Amongst the primitive water fungi chytrids are the most numerous, but the true water-moulds (Saprolegniales)

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* Ferdinandsen and Winge (1911).

are the most familiar. In all these Phycomycetes the zoospore is the normal unit of dispersal, and quite clearly such a spore is suitable only for the aquatic environment.

It is interesting to consider the biological value of the zoospore as contrasted with a non-motile spore. So far as actual transport is concerned the motility of the zoospore has little advantage over the non-motile spore, since the actual movement of water in a pond, lake, or stream is probably great in comparison with the feeble efforts of a zoid. The value of the zoospore would seem to reside in its power to 'select' the substratum on which it settles by virtue of its taxisms.*

Amongst the aquatic fungi derived apparently from terrestrial ancestors are Ascomycetes (Discomycetes, Pyrenomycetes, and some lichens) and Fungi Imperfecti, especially Hyphomycetes.

One striking and abundant flora of aquatic Hyphomycetes is regularly to be found on submerged, decaying leaves of deciduous trees and shrubs in well-aerated water, particularly in small streams that are not too sluggish. They occur especially on the petioles and larger veins, the branched septate mycelium ramifying in the decaying leaf tissue and the conidiophores projecting at right angles into the water. The whole story of dispersal is strictly aquatic, the spores being produced, liberated, and dispersed below water. Some twenty-five species of these fungi have been described† and most of them are very common (Fig. 79).

In aquatic Hyphomycetes the spores are hyaline and mostly of a somewhat unusual form. Most species have branched spores, and in these the commonest type is a spore consisting of four straight arms diverging from a common point. A study of spore development shows clearly that the mode of formation of the tetraradiate conidium differs

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* Müller (1911).

† Ingold (1942, 1943*a*, 1943*b*).

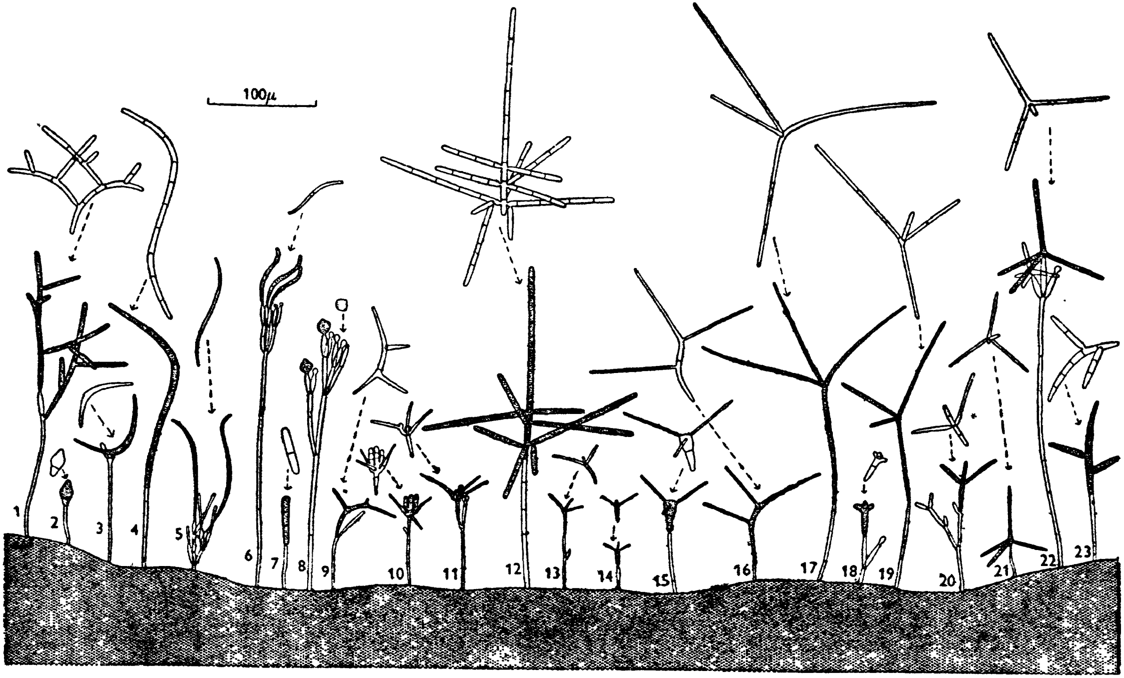

FIG. 79.

(For description see opposite)

markedly in different genera, suggesting strongly that parallel evolution has occurred and that this type of spore has some significance—some survival value—in the aquatic environment. This diversity of development of the tetraradiate spore may be illustrated by considering certain examples.

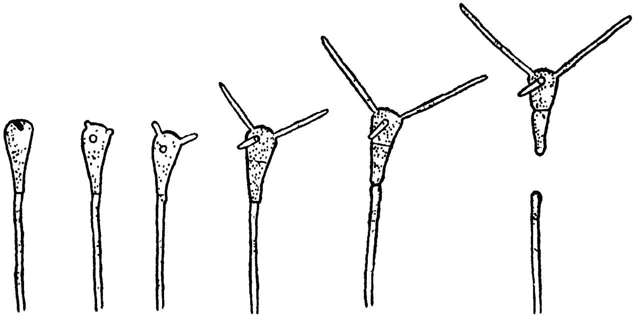

FIG. 80. *Clavariopsis aquatica.* Stages in spore development and liberation. × 350.

In *Clavariopsis aquatica* (Fig. 80) the spore-primordium is a club-shaped cell separated terminally from its conidiophore by a cross-wall. Then from the obtuse apex of this cell there appear simultaneously three little outgrowths which develop into three narrow arms, the original primordium forming the fourth, the shortest and fattest arm of the spore. As soon as the conidium is fully mature it

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FIG. 79. Aquatic Hyphomycetes of decaying leaves. Substratum of leaf tissue is indicated by stippling. For each species a single conidiophore is shown, the ripe, attached conidia being stippled. In addition a liberated spore of each species is illustrated. All are drawn to the same scale.

1, *Varicosporium elodeae*; 2, *Piricularia aquatica*; 3, *Lunulospora curvula*; 4, *Anguillospora longissima*; 5, *Flagellospora curvula*; 6, *F. penicillioides*; 7, *Piricularia submersa*; 8, *Margaritispora aquatica*; 9, *Tricladium angulatum*; 10, *Tetracladium setigerum*; 11, *T. marchalianum*; 12, *Dendrospora erecta*; 13, *Alatospora acuminata*; 14, *Heliscus longibrachiatus*; 15, *Clavariopsis aquatica*; 16, *Tricladium gracile*; 17, *Tetrachaetum elegans*; 18, *Heliscus aquaticus*; 19, *Articulospora inflata*; 20, *A. tetracladia*; 21, *Triscelophorus monosporus*; 22, *Lemonniera aquatica*; 23, *Tricladium splendens*.

separates from its conidiophore by disarticulation at the separating cross-wall.

In *Tetrachaetum elegans* (Fig. 81) the spore-primordium, as in *Clavariopsis*, is a single straight cell terminal on a simple conidiophore. The primordium increases by apical growth and, at a certain stage, two little protuberances appear side by side just behind the growing-point. The appearance of these causes the growing apex of the primordium to be deflected into a new direction, an angle of about 120° being formed between the original and the later directions of growth. The two protuberances and the original apical growing-point grow at the same rate until the mature four-armed spore is produced with all its arms of much the same length and width. By the time the spore

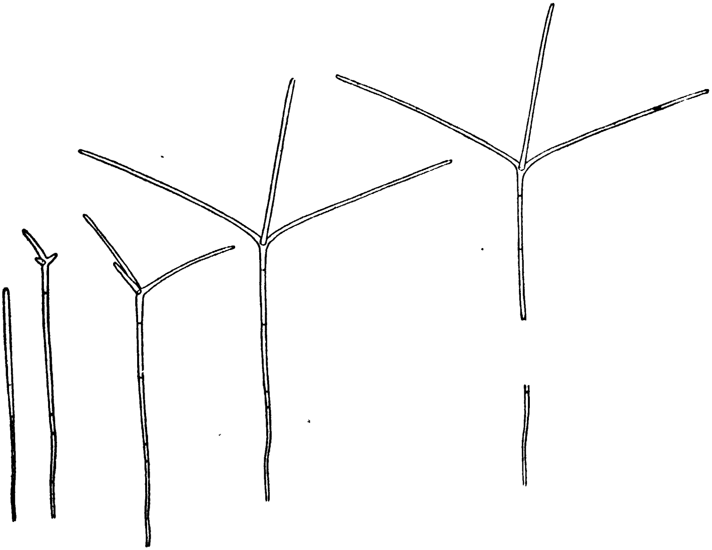

FIG. 81. *Tetrachaetum elegans*. Stages in spore development and liberation. × 210.

is fully grown a small separating cell has been cut off at the end of the conidiophore, and it is by the breakdown of this that the spore is liberated.

In the genus *Articulospora* two species have been described. *A. tetracladia* is very common but *A. inflata* is rarer. Both are characterized by the same type of development in which the four arms of the spore make their appearance in strict succession. In *A. inflata* (Fig. 82) the spore usually occurs singly at the end of a simple conidiophore. As in *Tetrachaetum* the spore-primordium is a straight cell with apical growth marked off by a wall from its conidiophore. When it reaches a certain length a cross-wall is formed delimiting a lower cell, which is the first-formed arm of the spore, from an upper which after further growth forms the second arm. Then, just below the wall separating these two arms, a small protuberance develops and begins to grow into the third arm. Much as in *Tetrachaetum* the development of this protuberance has the effect of bending the original straight hypha formed by the first and second arm. Still later a further outgrowth occurs below the septum dividing the first arm from the second and develops into

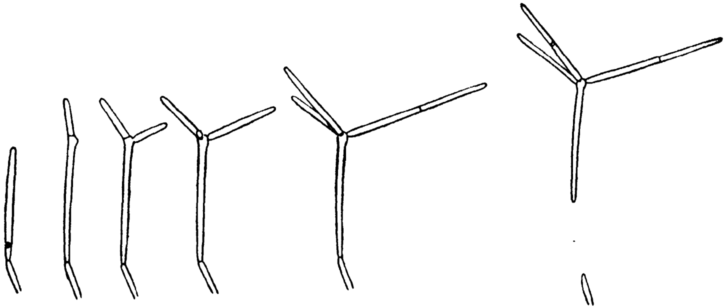

FIG. 82. *Articulospora inflata*. Stages in spore development and liberation. × 310.

the fourth arm. When all four arms are of approximately the same length the spore separates from its conidiophore as in *Clavariopsis*.

In *Clavariopsis*, *Tetrachaetum*, and *Articulospora* the mature spore is attached to the conidiophore by the tip of one of its four arms, but in two genera (*Lemonniera* and *Triscelophorus*) the attachment is at or near the point of divergence of the arms. Thus in the very common species *Lemonniera aquatica* the long conidiophore that juts out into the water is usually sparingly branched, terminating in a small group of spore-producing cells or phialides (Fig. 79, No. 22). The spore starts as a spherical primordium blown at the end of a phialide (Fig. 83), but soon becomes tetrahedral, each angle of the tetrahedron being a growing-point. Growth at these points takes place simultaneously and at the same rate until the arms are fully developed, when the spore separates, but only at the last moment is there formed a cross-wall between the spore and its phialide. As soon as one conidium is liberated another begins to form from the phialide. In *Lemonniera* the conidium is a phialospore whilst in *Clavariopsis*, *Tetrachaetum*, and *Articulospora* it is a terminal thallospore. However, the liberated spores of *Lemonniera aquatica*, *Tetrachaetum elegans*, and *Articulospora*

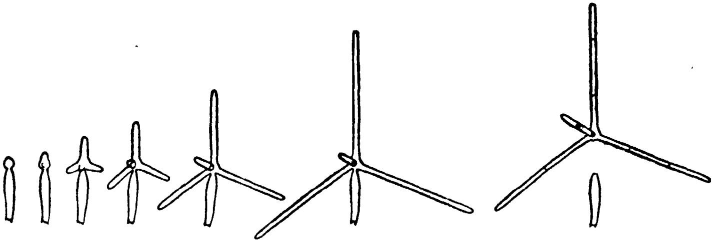

FIG. 83. *Lemonniera aquatica*. Stages in spore development and liberation. × 260.

inflata are so much alike that it is only after some experience that they can be told apart.

Triscelophorus monosporus (Fig. 84) agrees with *Lemonniera* in having its spore attached to its conidiophore near the point of divergence of its four arms, but differs in having a spore that is a terminal thallospore and in the fact that the arms arise in succession. The conidiophore is short and usually unbranched. The tip swells to form a spherical primordium delimited by a cross-wall. In this primordium apical growth is established, it becomes obclavate, and divides into an upper and a lower cell. By continued growth the upper cell develops into one long, straight arm of the spore whilst the others, arising in succession, bud out from the lower cell. When mature the tetraradiate terminal thallospore separates from its conidiophore as in *Clavariopsis*.

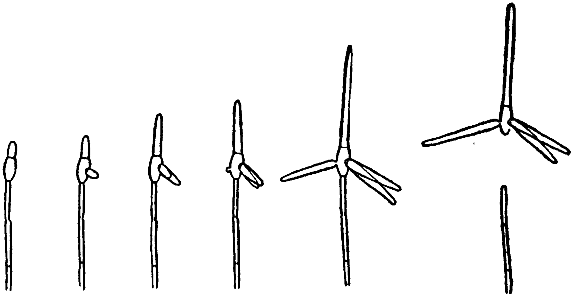

FIG. 84. *Triscelophorus monosporus*. Spore development and liberation. × 403.

These five examples of the different ways in which tetraradiate spores may arise suffice to support the view that this unusual kind of spore has evolved along a number of different lines of evolution. But other examples could be given. Thus in *Heliscus longibrachiatus* spore development is like that of *Clavariopsis*, and *Alatospora acuminata* like

Tetrachaetum, but in both species the spore is of the phialospore type, not a terminal thallospore.

It is of considerable interest that *Orbimyces spectabilis** (Fig. 85), a marine species, has branched conidia rather like those of the freshwater aquatic Hyphomycetes. Further, in *Sphacelaria*, a genus of brown seaweeds, certain species reproduce largely in a vegetative manner by propagules, which are branches of limited growth and definite form that are shed when mature. In *Sphacelaria fusca* (Fig. 86) these are tetraradiate and show an extraordinary agreement with the spores of such Hyphomycetes as *Tetrachaetum*, *Articulospora*, and *Lemonniera*.

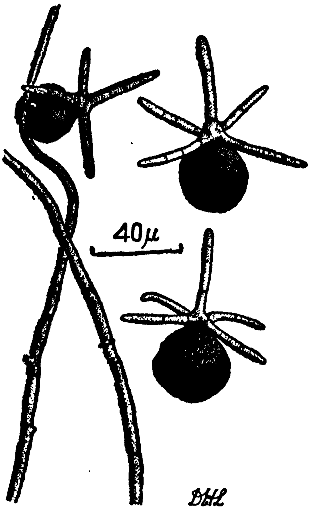

FIG. 85. *Orbimyces spectabilis*. After Linder. Two liberated spores and one still attached to its parent mycelium.

The tetraradiate reproductive unit is not limited to aquatic organisms. It occurs, for instance, in *Tetraploa aristata* whose spores, as recorded long ago by Cunningham, may be air-borne.† However, in aquatic Hyphomycetes the tetraradiate spore is of such frequent occurrence that it is natural to suppose it has some biological significance in the aquatic environment. What this significance may be is pure speculation. Perhaps a spore of this kind settles relatively slowly in water and so stands a good chance of adequate dispersal; perhaps, on the other hand, it acts as an anchor and readily

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* Barghoorn and Linder (1944).

† Cunningham (n.d.).

becomes entangled in a suitable substratum, for the arrest of a spore in a stream may be a real problem; or perhaps it is not so easily devoured by small aquatic animals as a spherical or oval spore would be.

Another type of spore common amongst the Hyphomycetes of submerged decaying leaves is the long filamentous or vermiform spore, twisted so that its curvature lies in more than one plane (Fig. 87). Two species are very common: *Anguillospora longissima* where the conidium is a terminal thallospore, and *Flagellospora curvula* where it is a phialospore. Very probably the long filamentous spore has the same biological significance as the tetraradiate type, and it is of interest that other aquatic fungi, for example the fresh-water discomycetes *Apostemidium guernisaci* and *Vibrissea truncorum*, and the marine pyrenomycete *Halophiobolus salinus* also have spores of this shape. However, it must be borne in mind that many terrestrial fungi have long, thread-like spores (e.g. *Cordyceps militaris* and *Rhytisma acerinum*). However, in this connexion it is a suggestive

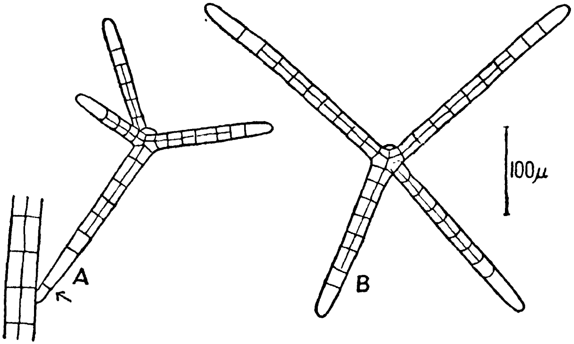

FIG. 86. *Sphacelaria fusca.*

A, portion of thallus with propagule attached: arrow indicates where separation will occur; *B*, liberated propagule.

fact that in *Zortera*, the only British genus of flowering plants with pollination occurring below water, the pollen grains are long and filamentous (Fig. 87, *G*).

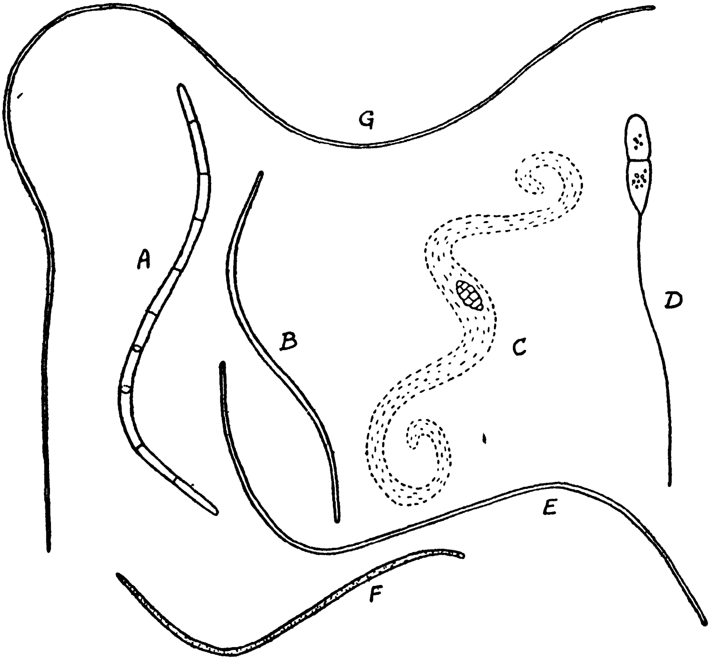

FIG. 87. Some water-dispersed units of elongated form.

Conidia: ***A*, *Anguillospora longissima***, × 316. *B*, ***Flagellospora curvula***, × 436. Ascospores; *C*, ***Pleospora scirpicola***, × 65. *D*, ***Loramyces juncicola***, × 672. *E*, ***Apostemidium guernisaci***, × 428. *F*, ***Halophiobolus salinus***, × 170. Pollen grain: *G*, *Zostera marina*, × 63.

There is another widespread flora of aquatic Hyphomycetes which occurs on submerged leaves decaying under conditions that appear to be almost anaerobic.* Leaves of deciduous trees dredged from the bottom of stagnant ponds or lakes have a characteristic black appearance. If

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* Glen-Bott (1951); van Beverwijk (1951).

these leaves are subsequently kept damp but exposed to air in petri dishes in the light, they soon develop glistening white or pale yellow spots, each representing a spore or spore-cluster. The fungi concerned belong to such genera as *Helicodendron* (Fig. 88), *Helicoon*, and *Clathrosphaerina*. Apparently, in the submerged leaves the mycelium grows, though somewhat slowly, in spite of the anaerobic or nearly anaerobic conditions. However, sporulation can occur only in the presence of a gas phase, but the gas is not necessarily air, since, at least in some species, growth and sporulation can take place in pure cultures on malt agar grown in an atmosphere of nitrogen. These particular fungi of submerged decayed leaves are not confined to the aquatic habitat, though that appears to be their characteristic environment. They have also been found under subaerial conditions on damp, rotten wood. The most striking feature of the spores is that they are not readily wettable. They float on water, helped by the fact that the spores are built in the form of a helix or spherical network in which air is enmeshed and not easily displaced. In nature it is probable that sporulation occurs when blackened leaves containing the mycelium of these fungi are exposed, as, for example, around the edge of a drying pond. When the water-level

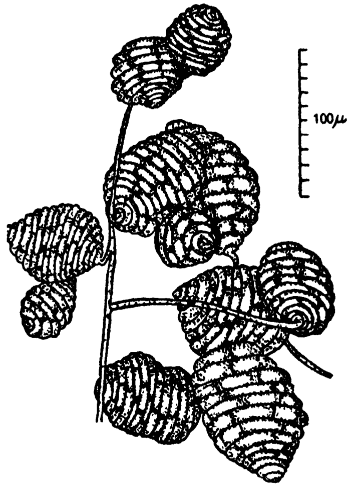

FIG. 88. *Helicodendron giganteum.* Branched conidiophore bearing primary conidia which may give rise to secondary conidia. (After Glen-Bott (1951)).

again rises the leaves are submerged but the spores are left floating. Some species (e.g. *Helicodendron triglitziensis*) can sporulate even when the leaves are submerged so long as the water is only a few centimetres deep. Under these conditions fine hyphae grow up to the surface and produce spores there. Although wind dispersal of the spores of these fungi can obviously occur, it seems likely that they are usually dispersed on the surface of the water. Falling on to the water and floating there, leaves become infected, and when they become waterlogged and sink growth of the fungi continues.

In addition to Hyphomycetes, quite a large number of minute Ascomycetes are submerged aquatic fungi. These are so widely scattered in any 'natural' scheme of classification that it seems clear they are not primitive aquatic fungi, but are almost certainly derived from terrestrial ancestors.

In the fresh-water habitat minute Discomycetes and Pyrenomycetes are common on submerged dead stalks of reed-swamp plants (e.g. *Phalaris arundinacea*, *Phragmites communis*, *Scirpus lacustris*, *Equisetum fluviatile*) and on submerged, waterlogged twigs and branches of trees. These fungi are little different from those occurring on land, but the spores tend to have certain features that seem to stamp them as belonging to aquatic organisms. Thus the ascospores may have well-developed mucilage sheaths or appendages. They are often considerably elongated and are almost always densely crowded with minute oil globules. Perhaps here again spores with these features may settle comparatively slowly, and perhaps the mucilage may be important in connexion with anchorage.

It is to be noted that asci, whether arranged in an apothecium or a perithecium, can function quite well under water. On the other hand, the basidium is an apparatus suited only to sub-aerial conditions, and it is a striking fact that submerged aquatic Basidiomycetes are unknown. On the whole, spore liberation is similar in aquatic and land Ascomycetes. Thus, in the submerged aquatic *Ophiobolus typhae* (Fig. 89), a saprophyte on the leaf-bases of *Typha latifolia*, spore liberation* from the perithecium is of the detached-ascus type already described for terrestrial Pyrenomycetes. Again, in *Pleospora scirpicola*, in which spore discharge was illustrated nearly a hundred years ago by Pringsheim,† the mechanism is of the jack-in-the-box type (p. 35). Although Pringsheim gave such a clear and beautiful account of successive spore discharge from the ascus in this common aquatic fungus, he failed to note the extraordinary development of the mucilage sheath around the spore. This can best be seen if freshly liberated ascospores are mounted in indian ink. When the spores are first freed from the ascus the sheath is comparatively small and is bounded by a firm membrane, but following

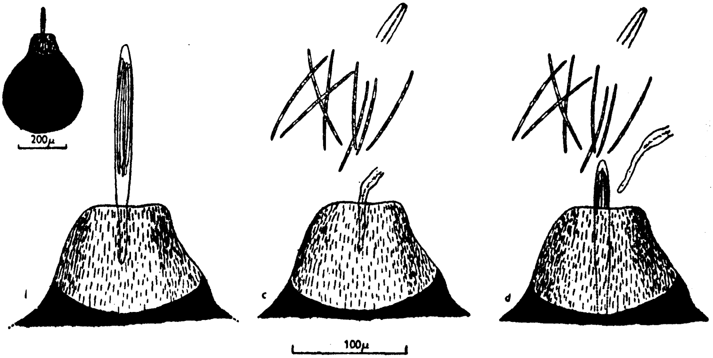

FIG. 89. *Ophiobolus typhae*. Spore discharge in water.

A single perithecium is shown at low power (*a*) and the neck region more highly magnified (*b*). *b*, *c*, and *d* show stages in the process. A few seconds elapsed between *b* and *d*.

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* Ingold (1951).

† Pringsheim (1858).

discharge the mucilage rapidly absorbs water so that a long, worm-like strand of fluid mucilage, about half a millimetre long, is formed containing the large spore. Again, in the minute pyrenomycete *Loramyces juncicola*,* occurring on submerged dead stalks of *Juncus* spp. and *Scirpus lacustris*, the two-celled ascospore is surrounded by a thick mucilaginous sheath and, in addition, the lower cell is prolonged into a long, straight tail, so that at a glance the spore looks like a large chytrid zoospore. In these two fungi and in others like them the mucilage is of a very fluid nature and after a short time the sheaths disappear completely, but in *Ceriospora caudae-suis*,† a saprophyte on submerged sticks of ash, there is a coiled, tendril-like appendage of persistent mucilage at each pole of the spore.

Turning to the marine Ascomycetes, there are two distinct biological types. To one type belong those species that grow as saprophytes on submerged wood and cordage: species of the other type are parasites of the larger seaweeds. Knowledge of the saprophytic species comes mainly from the work of Barghoorn and Linder.‡ The saprophytic lignicolous forms show a striking parallelism with the fresh-water Ascomycetes. In some species (*Halophiobolus* spp.) the spores are long and thread-like and in addition are furnished with adhesive tips. In others, although the spores are not thread-like, they have various types of mucilaginous appendage (Fig. 90). Linder suggests that these modifications 'appear to serve both for the attachment of spores to the substratum, as well as to assist in suspending the spores in water and facilitating their dispersal'. He notes how successfully the sticky extremities attack the spores of *Halophiobolus* spp. to an object, and because of this it is very difficult to discharge spores from a glass

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* Weston (1929).

† Ingold (1951).

‡ Barghoorn and Linder (1944).

pipette. A feature noted by Linder in all the saprophytic marine Pyrenomycetes was the breakdown of the ascus wall at maturity. Apparently in these marine species the original method of discharge has been lost and the spores ooze out in a mucilaginous mass. This type of spore liberation may occur in the fresh-water Pyrenomycetes, but it is by no means general.

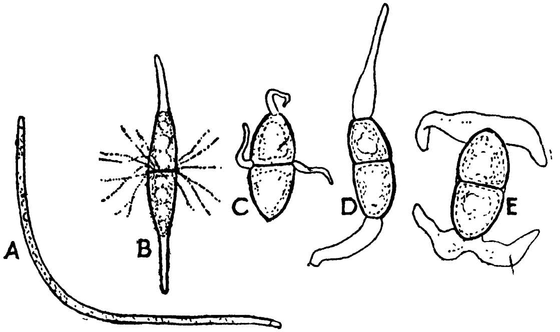

FIG. 90. Ascospores of marine saprophytic Pyrenomycetes with slimy appendages.

A, Halophiobolus opacus, × 212. *B, Peritrichospora integra,* × 500. *C, Halosphaeria appendiculata,* × 400. *D, Ceriosporopsis halima,* × 500. *E, Remispora maritima,* × 500. (After Barghoorn and Linder (1944)).

Knowledge of the Pyrenomycetes that attack the larger seaweeds is due largely to the work of Cotton* and of Sutherland.† Some of these fungi also have long, worm-like spores, for example *Ophiobolus laminariae*, a parasite found on the stipe of *Laminaria digitata* and *Trailia ascophylli*, which attacks *Ascophyllum*. One of the most interesting of these marine species is *Mycosphaerella ascophylli*. This causes a systemic infection of *Ascophyllum* and apparently it is invariably present in the host plant. However, the production of perithecia is limited to the receptacles. Ascospores

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* Cotton (1907).

† Sutherland (1915 *a, b, c*).

of the parasite and eggs of the seaweed are liberated at the same time, and no doubt infection of the young seaweed occurs at a very early stage in its career, although the story of infection has yet to be told.

Much remains to be discovered concerning the dispersal of water fungi. Further information is needed about the mechanism of spore liberation from the perithecia of aquatic Ascomycetes, especially those in which deliquescence of the asci occurs. Observations on the rate of fall of the spores in water might yield interesting information, and a study of how readily spores adhere to underwater objects would be of special interest.

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APPENDIX

List of Fungi, Giving the Authority for Each Species

Alatospora acuminata Ing.
Aleuria repanda (Pers. ex Fr.) Gill
A. vesiculosa (Bull. ex Fr.) Bond.
Anguillospora longissima (de Wild.) Ing.
Apostemidium guernisaci (Cr.) Durand
Armillaria mellea (Vahl.) Fr.
Arthobotrys oligospora Fres.
Articulospora inflata Ing.
A. tetracladia Ing.
Ascobolus magnificus Dodge
A. stercorarius (Bull.) Schroet.
Ascochyta pisi Libert
Aseroe rubra Labill
Ashbya gossypii (Ashby and Now.) Quill.
Aspergillus niger van.Tiegh.
Auricularia mesenterica (Dicks.) Fr.
Basidiobolus ranarum Eidam
Boletus chrysenteron (Bull.) Fr.
Botrytis anthophila Bond.
B. cinerea Pers.
Bullera alba (Hanna) Derx
Calvatia gigantea (Batsch ex Pers.) Lloyd
Candida reukaufii (Grüss) Diddens and Lodder
Ceratostomella ampullasca (Cooke) Sacc.
C. ips Rumbold
Ceriospora caudae-suis Ing.
Ceriosporopsis halima Linder.
Chaetomium cochliodes Palliser
Ciliaria scutellata (Linn. ex Fr.) Quél.
Cladonia pyxidata Hoffm.
Cladosporium herbarum Link ex Fr.
Clathrus cancellatus (Tourn.) L.
Clavaria cinerea Bull.
C. inaequalis Muller
C. pistillaris L.
Clavariopsis aquatica de Wild.
Claviceps purpurea Tul.
Colletotrichum lindemuthianum (Sacc. & Magn.) Bri. & Cav.
C. linicola Pethybr. & Laff.
Collybia velutipes (Curt.) Fr.
Coprinus atramentarius (Bull.) Fr.
C. curtus Kalch.
C. fimetarius Fr.
C. micaceus (Bull.) Fr.
C. plicatilis (Curt.) Fr.
C. sterquilinus (Fr.) Cke.
Cordyceps militaris (L.) Link
Corticium filamentosa Bk. & Curt.
Cronartium ribicola F. de Waldh.
Crucibulum vulgare Tul.
Cryptoporus volvatus (Pk.) Hulb.
Cunninghamella elegans Lend.
Cyathus stercoreus (Schw.) de Toni
C. striatus Pers.
Dacryomyces deliquescens (Bull.) Duby
Daldinia concentrica Ces. & de Not.
Dasyobolus immersus (Pers. ex Fr.) Sacc.

Dendrospora erecta Ing.
Diatrype disciformis (Hoffm. ex Fr.) Fr.
D. stigma (Hoffm. ex Fr.) Fr.
Elaphomyces granulatus Fr.
Empusa muscae (Fr.) Cohn
Endothia parasitica (Murr.) And. & And.
Entomophthora coronata (Cost.) Kevorkian
E. sphaerosperma Fres.
Epichloe typhina (Pers. ex Fr.) Tul.
Flagellospora curvula Ing.
F. penicillioides Ing.
Fomes fomentarius (L.) Gillet
F. ulmarius (Sow.) Fr.
Fusarium lini Rolley
F. moniliforme Sheldon
Galactinia badia (Pers. ex Fr.) Bond.
Ganoderma applanatum (Pers.) Pat.
Geoglossum ophioglossoides (L.) Sacc.
Gliocladium roseum Bain
Gliomastix convoluta (Harz) Mason
Gnomonia rubi (Rehm) Wint.
Gymnosporangium juniperi-virginianae Schw.
G. nidus-avis Thaxt.
Halophiobolus opacus Linder
H. salinus Linder
Halosphaeria appendiculata Linder
Helicodendron giganteum Glen-Bott
H. triglitziensis (Jaap) Linder
Heliscus aquaticus Ing.
H. longibrachiatus Ing.
Helminthosporium avenae Eidam
H. gramineum Rabenh.
H. sativum Pammel, King, & Bajje
Hirneola auricula-judae (L.) Berk.
Hydnum repandum L.
Hypoxylon coccineum Bull.
H. fuscum (Pers. ex Fr.) Fr.
H. pruinatum (Klotszch) Ell. & Ev.
Lemonniera aquatica de Wild.
Lenzites betulina (L.) Fr.
Leptopodia elastica (Bull. ex Fr.) Bond.
Leptosphaeria acuta (Hoffm. ex Fr.) Karst.
Loramyces juncicola Weston
Lunulspora curvula Ing.
Lycoperdon perlatum Pers.
L. pyriforme (Schaeff.) Pers.
Margaritispora aquatica Ing.
Melampsora lini (Ehrenb.) Lév.
Melastiza miniata (W. G. Sm.) Bond.
Microsphaera alni-extensa (Cke. & Pk.) Salm.
Mitrula phalloides (Bull.) Chev.
Morchella rotunda (Pers.) Bond.
Mucor hiemalis Wehm.
M. racemosus Fres.
Mutinus caninus (Huds. ex Pers.) Fr.
Mycosphaerella ascophylli Cotton
Nectria cinnabarina (Tode ex Fr.) Fr.
Neurospora sitophila Shear & Dodge
Nyctalis asterophora Fr.
N. parasitica (Bull.) Fr.
Omphalia flavida (Cke.) Maubl. & Rangel
Ophiobolus laminariae Sutherland
O. typhae Feltg.
Ophiostoma ulmi (Buisman) Nannf.
Orbimyces spectabilis Linder

Paxillus involutus (Batsch.) Fr.
Penicillium notatum Westling
Peritrichospora integra Linder
Peronospora parasitica (Pers.) de Bary
P. tabacina Adam
Pertusaria velata Nyl.
Peziza aurantia Pers. ex Fr.
Phallus impudicus L. ex Pers.
Phialea temulenta Paill. & Delacr.
Phycomyces blakesleeanus Burg.
Phytophthora infestans (Mont.) de Bary
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Pilobolus kleinii v. Tiegh.
P. longipes v. Tiegh.
Piricularia aquatica Ing.
P. submersa Ing.
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Pleospora scirpicola (DC. ex Fr.) Karst.
Podosphaera leucotricha (Ell. & Everh.) Salm.
Polyporus betulinus (Bull.) Fr.
Polyspora lini Laff.
Protomyces inundatus Dang.
P. macrosporus Unger
P. pachydermus Thüm
Psalliota campestris (L.) Fr.
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P. helianthi Schw.
P. malvacearum Mont.
P. suaveolens (Pers.) Rostr.
P. taraxaci Plowright
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R. ochroleuca Fr.
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S. libertiana Fuckel
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S. scirpicola Rehm
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S. curvula de Bary
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U. hordii (Pers.) Lagerh.
U. nuda (Jens.) Rostr.
U. succisae Magn.
U. violacea (Pers.) Fuckel
U. zeae (Beckm.) Unger
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