FUNGAL SPORES

Their Liberation and Dispersal

FUNGAL SPORES

Their Liberation and Dispersal

C. T. INGOLD

CLARENDON PRESS · OXFORD

1971

Oxford University Press, Ely House, London W. 1
GLASGOW NEW YORK TORONTO MELBOURNE WELLINGTON
CAPE TOWN SALISBURY IBADAN NAIROBI DAR ES SALAAM LUSAKA ADDIS ABABA
BOMBAY CALCUTTA MADRAS KARACHI LAHORE DACCA
KUALA LUMPUR SINGAPORE HONG KONG TOKYO

PRINTED IN GREAT BRITAIN
AT THE PITMAN PRESS, BATH

PREFACE

INSTEAD of providing second editions of *Dispersal in Fungi* and *Spore Liberation*, I decided to unite the two into a single work, omitting, however, the discussion of bryophytes that occurs at the end of the latter. Initially an exercise involving scissors and paste was envisaged, but it soon appeared that this was not suitable, and a complete re-writing had to be undertaken. This is largely because so much has been done in the general field of dispersal in fungi during the past decade. Further, although many illustrations from the earlier books are included in the present one, it was necessary to provide over 80 new ones.

Although a large proportion of the illustrations are my own, many are from other authors and I am grateful to them for allowing me to reproduce their figures. Further, I have to thank the Director of the Royal Botanic Gardens, Kew for permission to use two previously unpublished drawings by the late Professor A. H. R. Buller, that occur in the typescript of an unpublished volume of his *Researches* bequeathed to Kew. My thanks are also due to the Hafner Publishing Company who have given permission to reproduce certain figures from Buller's published volumes. I am also indebted to Dr. A. D. Greenwood for allowing me to reproduce stills from his film of *Saprolegnia*.

I believe that students of fungi will always be interested in questions of spore dispersal, but we are now in an age when the study of mechanisms is nearing its end, and emphasis will probably be on the extension of knowledge by the quantitative evaluation of dispersal in the overall ecological picture of fungi in field situations.

Birkbeck College
London, 1970.

C. T. INGOLD

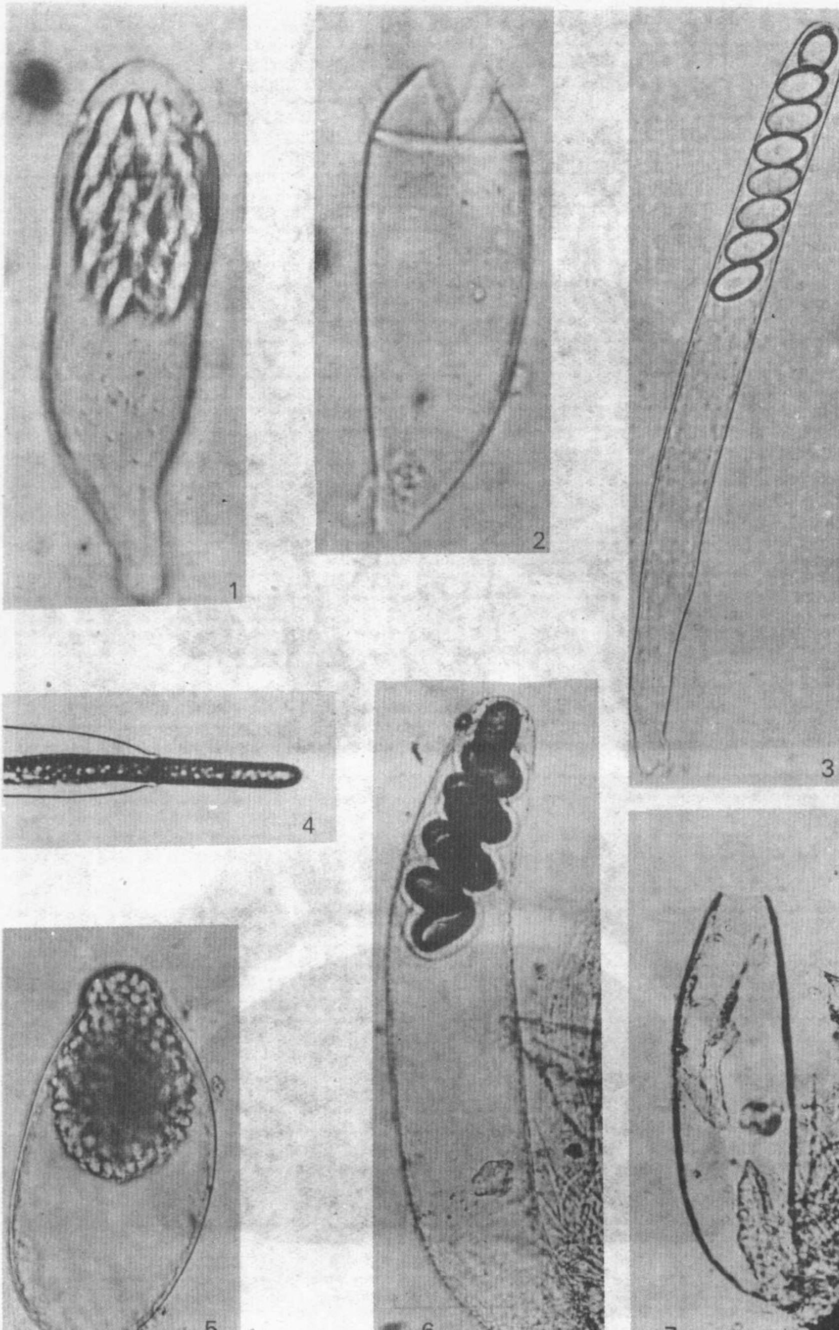


PLATE I. Asci. 1, 2, *Ascozonus woolhopensis*, a ripe ascus and a discharged ascus; note ring of thickening near top of ascus. × 700. 3, *Pyronema omphalodes*, ripe ascus. × 500. 4, *Geoglossum* sp., ascospore escaping from the ascus. × 260. 5, *Rhyparobius nanus*, multispored ascus. × 500. 6, 7, *Dasyobolus immersus*, mature ascus with purple spores surrounded by mucilage sheaths and the same ascus a few moments later after discharge. × 140.

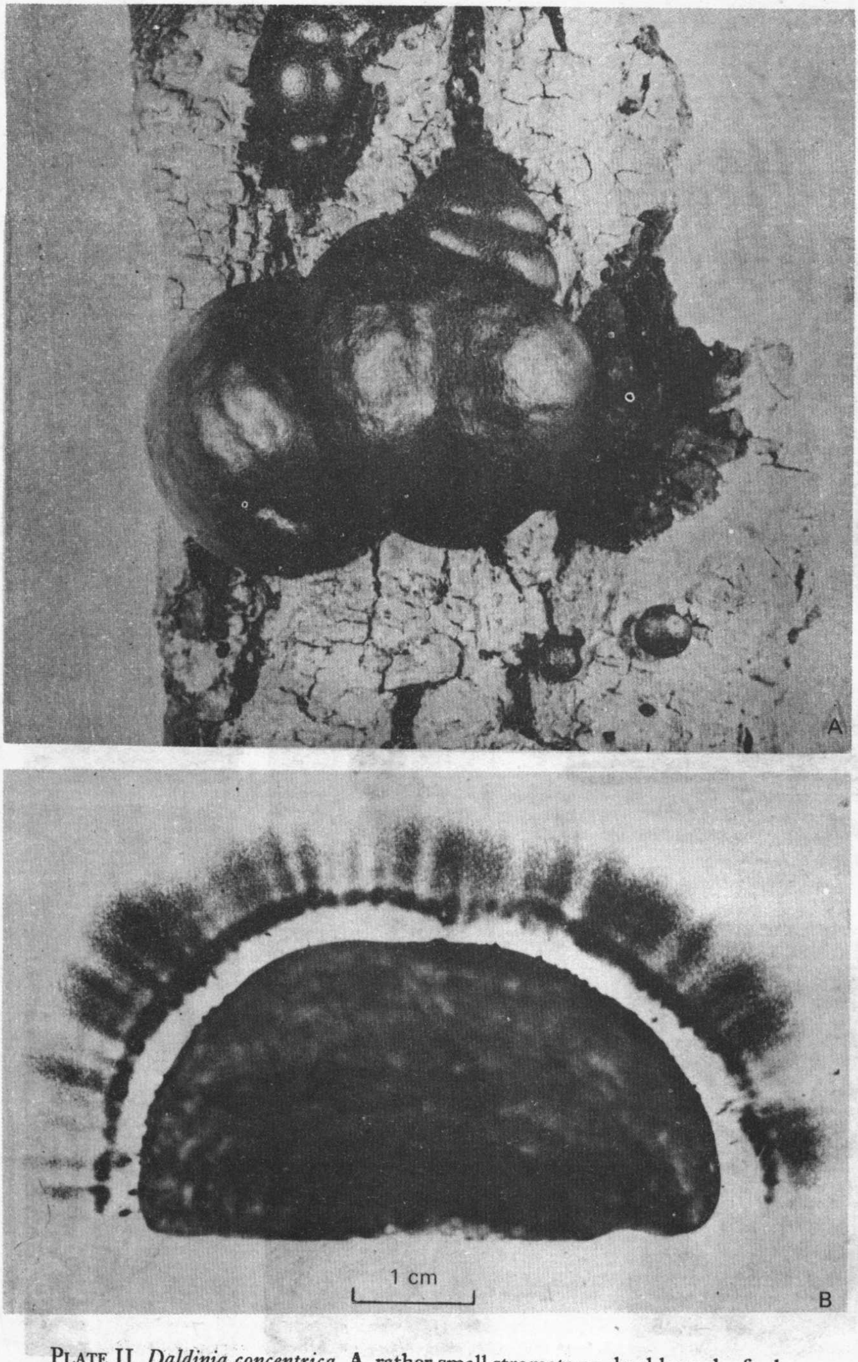
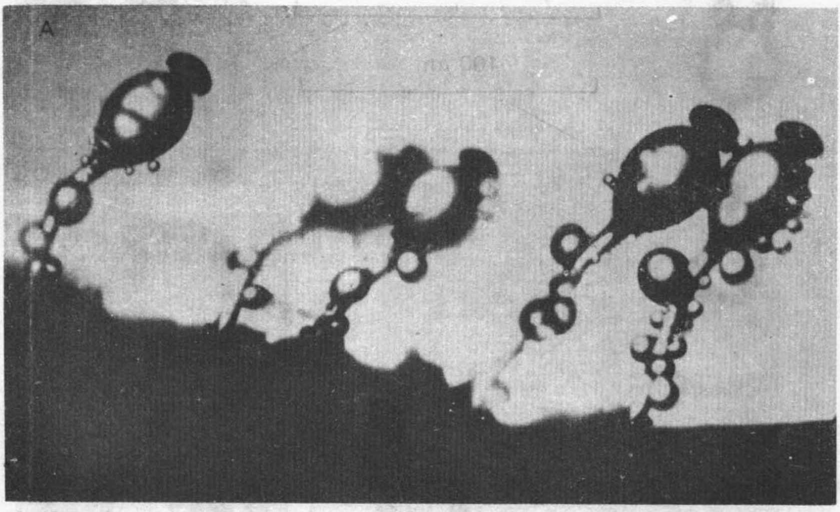


PLATE II. *Daldinia concentrica*. **A**, rather small stromata on dead branch of ash (*Fraxinus*). **B**, spore deposit, showing zoning, accumulated overnight around a thick median slice of a largish stroma lying horizontally on a glass plate.



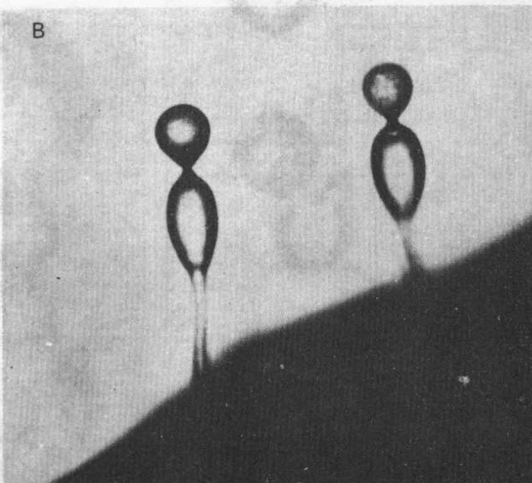


PLATE III. A, *Pilobolus kleinii*, sporangiophores on horse dung. ×12. B, *Basidiobolus ranarum*, conidiophores on the excrement of frogs. ×260.

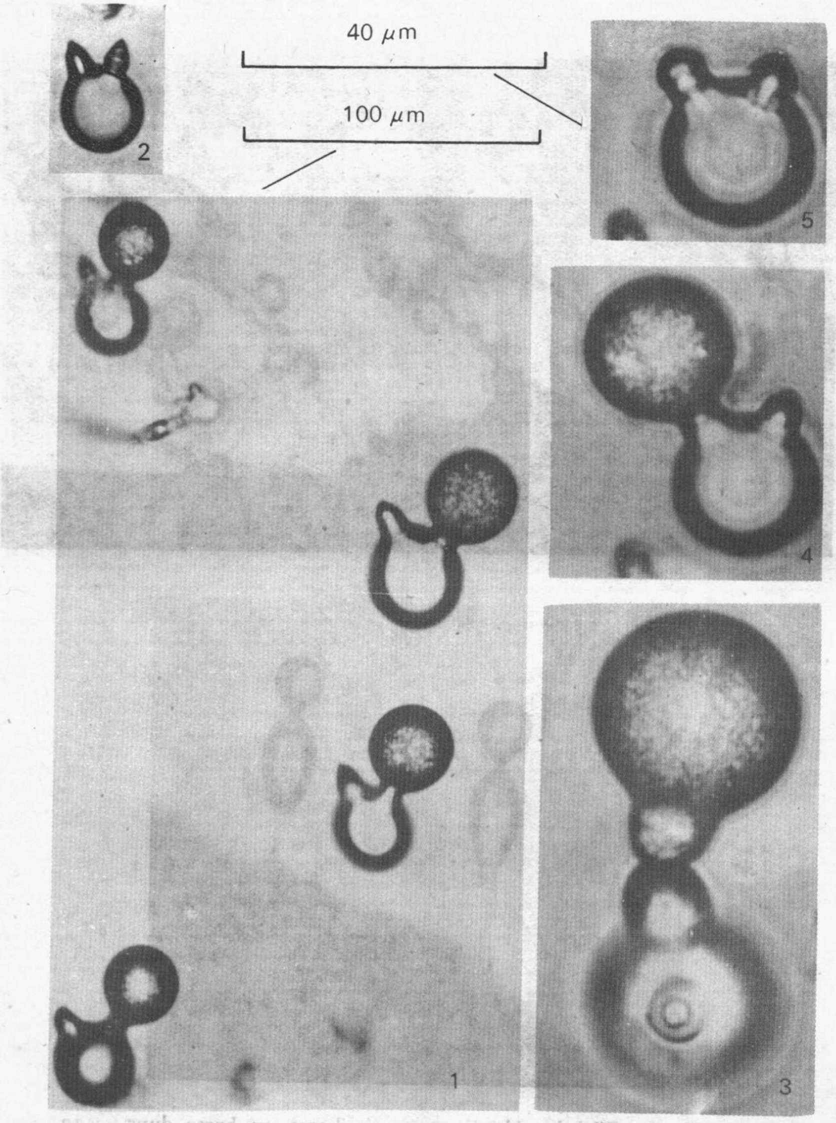


PLATE IV. *Conidiobolus coronatus*. Discharged conidia on water agar, 3 h after discharge, which have germinated to produce secondary conidia. 1, Four conidia each with a ripe secondary conidium (produced towards the light); the projection to the left of each being the everted papilla of the orginal spore produced at the moment of discharge. 2, Topmost spore of the four in the previous figure when the secondary spore has been discharged (note the fortuitous resemblance of the vacated conidiophore and the everted papilla of the parent spore). 3, A secondary conidium where the papilla has become everted but not vigorously enough to discharge the spore; the everted papilla of the primary spore is seen in surface view. 4, An empty primary conidium with its papilla on right and with a ripe secondary conidium on the left. 5, The same a few minutes later.

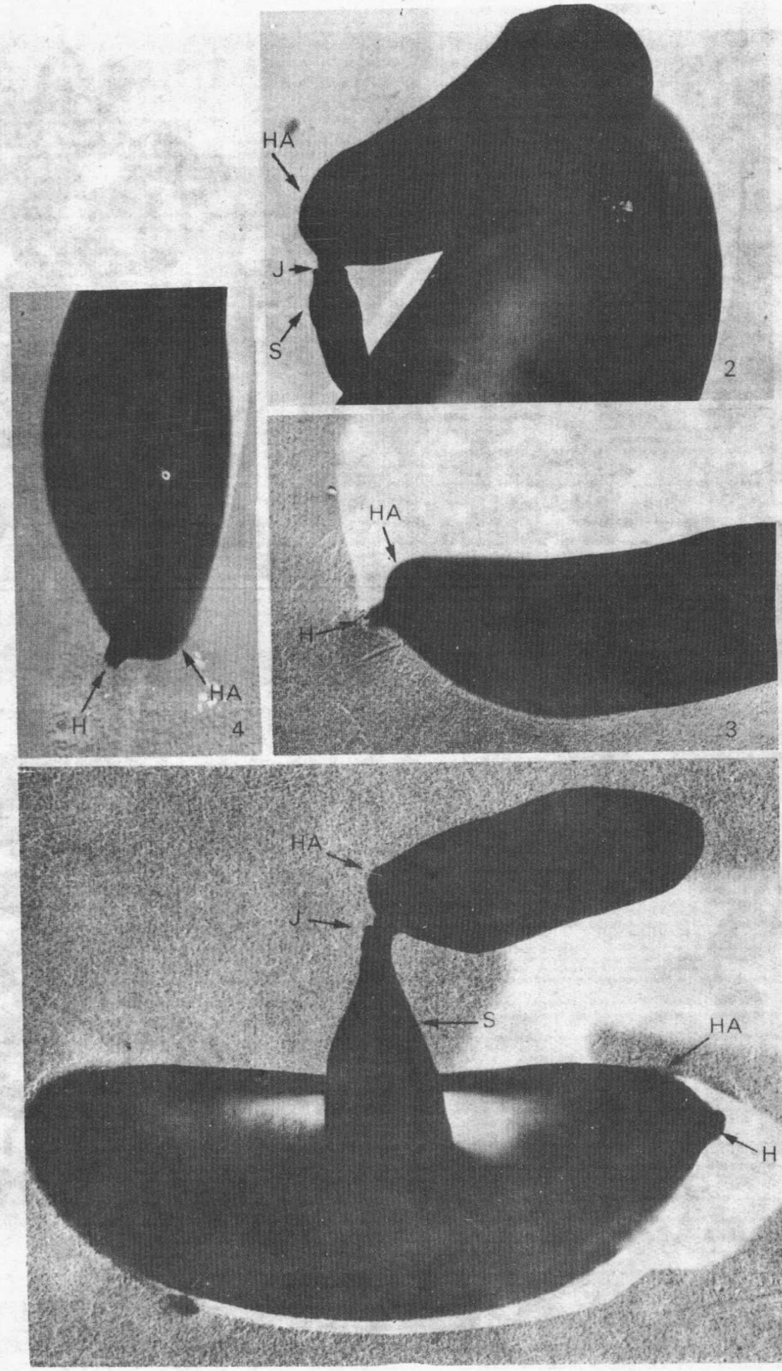


PLATE V. *Sporobolomyces roseus.* Electron micrographs of dried and shadowed specimens. 1, 2, Discharged ballistospores that have germinated by a sterigma (S) to produce a secondary ballistospore. 3, 4, Freshly discharged ballistospores. H, hilum; HA, hilar appendix; J, junction of spore and sterigma. × 14 000.

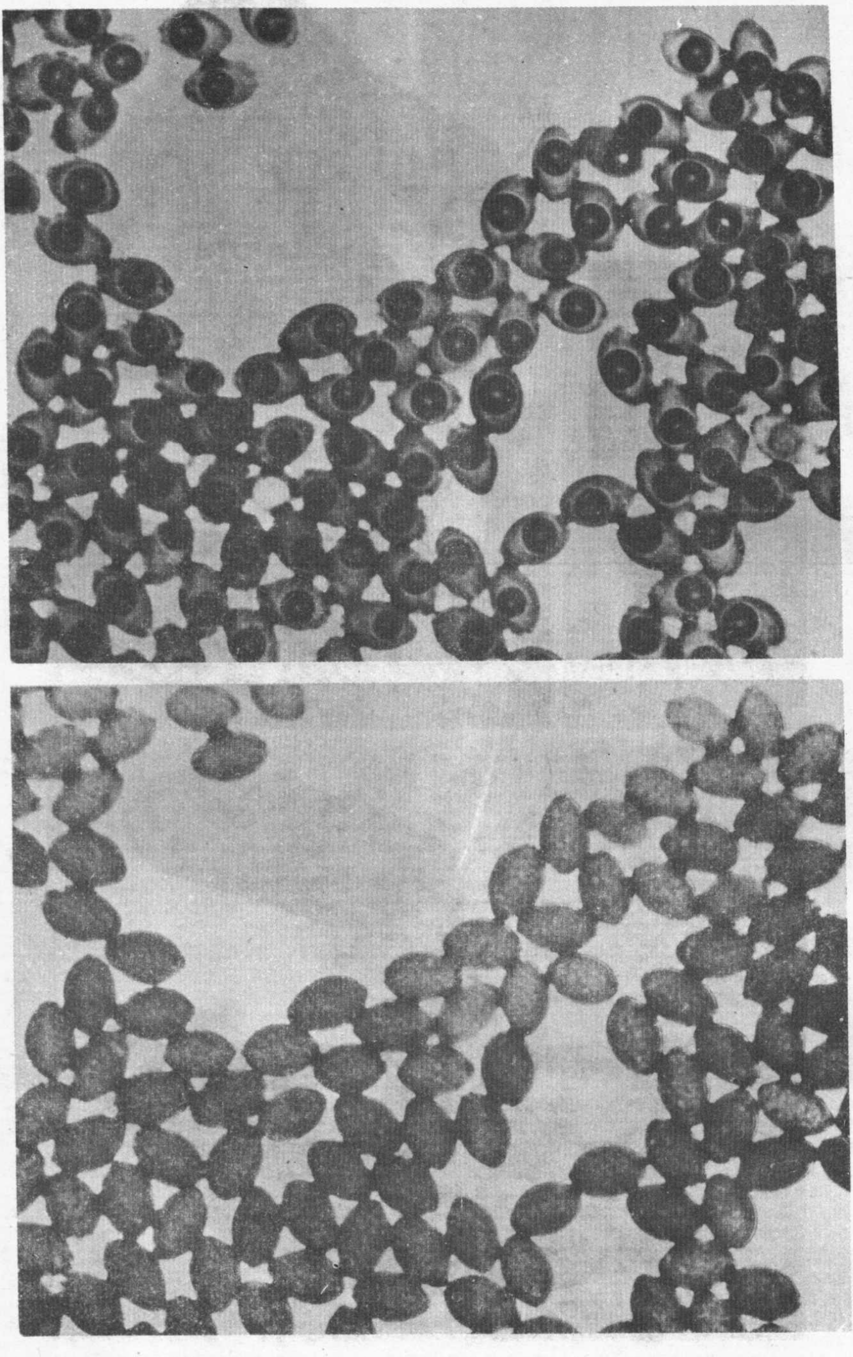


PLATE VI. *Podospora curvicolla*. Above: freshly discharged spores caught on a dry slide photographed 20 s after flooding with water; each contains a gas bubble. Below: the same spores 60 s later; the gas phase has disappeared. ×630.

PLATE VII. *Sphaerobolus stellatus*. Group of fruit-bodies as seen under a simple lens. In some the dark glebal-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. The two bright spots appearing in the undischarged fruit-body are images of lamps used in the photography.

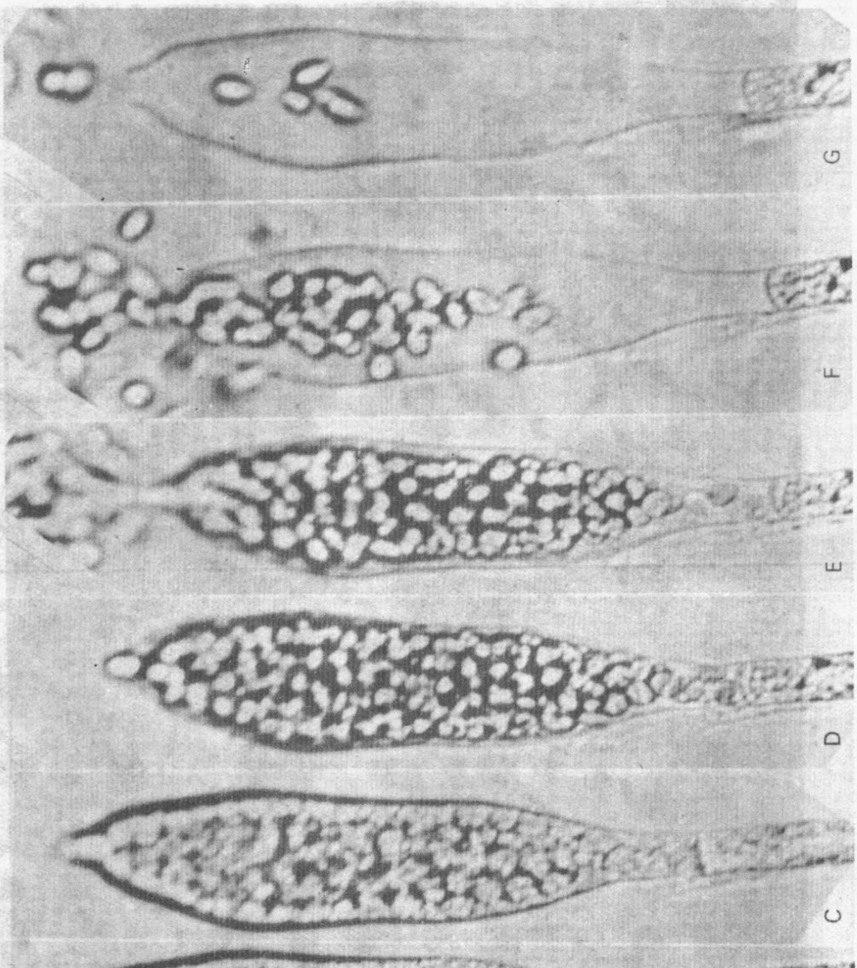


PLATE VIII. *Saprolegnia ferax*. Maturation of zoosporangium and release of zoospores. A, swollen hyphal tip with large central vacuole but no delimiting basal cross-wall. B, basal cross-wall formed and apical papilla developed. C and D, zoospore delimitation. E, F, and G, stages in spore escape. Only a few seconds separate stage D from stage G. × approx. 500. Stills from a film by Dr. D. Greenwood.

CONTENTS

I. INTRODUCTION

THIS book is concerned with the liberation and dispersal of fungal spores, but before turning our attention to the processes involved it is important to consider the actual necessity for dispersal.

Dispersal seems to be a problem for all kinds of organism. Each species of plant or animal occurs in a circumscribed geographical area; it has a fairly definite range. This may be of small extent. Indeed a species may be limited to one isolated little island or to a single mountain top. On the other hand it may range over almost the whole of the habitable world. Even where the range is now great, the species almost certainly started in one spot. It has been argued that the widely-ranging species tend to be the older, while comparable species that at present occupy small areas tend to be young beginners. Extension of geographical range is a feature of the history of each species and for this extension some mechanism of dispersal is a necessity.

Most animals exploit their immediate territory and extend their range by their own movements, but the fixed organism, whether an animal such as a sponge or coral, or a plant, must rely on detachable units for dispersal. Sponges and corals have their free-swimming larval stages, flowering plants their seeds, and fungi, ferns, mosses, liverworts, and seaweeds their microscopic spores.

The necessity for dispersal is not confined to the extension of geographical area. Individuals within the general range of each species are usually limited to certain ecological niches and if these are scattered the dispersal mechanism must be adequate to provide propagules in the right places when and where opportunities offer.

Again, dispersal has a genetic importance. Each species at any time is more or less in equilibrium with its environment, both physical and biotic. But this environment may change over the years and a species, if it is to survive, must be capable of adjusting itself to these altering conditions. Here the degree of genetic variability available for selection may be of great importance. Dispersal may be of significance in giving the opportunity for new variability, when it arises in a species at a certain point in its range, to spread among the whole population. This spread of new variability may be achieved by the dispersal of reproductive units, such as seeds and spores, capable of giving rise to new individuals, but it may also be achieved by the spread of pollen grains in higher plants. A similar example from the fungi is the dispersal of pycniospores of rusts which can, like pollen grains, transport genes, but cannot grow directly into new individuals. It should be noted, however, that although efficient dispersal may spread new genes among a population and so increase the evolutionary plasticity of a species, it tends to operate against actual speciation, since effective dispersal breaks down isolation on which species differentiation so largely depends.

To sum up, it may be said that dispersal is of significance for the maintenance of the population within its existing range, for the extension of the range of a species, and for its genetical development.

Fungi reproduce and spread mainly by spores. These, as in other cryptogams, are microscopic units mostly unicellular although not infrequently multicellular and containing some food reserve, usually oil or glycogen. Many fungal spores are meiospores, as in bryophytes and pteridophytes, with a meiosis involved in their formation. Ascospores, basidiospores, and the spores in the sporangia of Mycetozoa are of this nature. However, spore production may be quite unrelated to meiosis. This is true, for example, of the great range of conidial forms classified in Fungi Imperfecti, of the conidial stages of Ascomycetes, of the urediospores of Uredinales (rusts), and of the sporangiospores of Mucorales.

Nearly all spores are essentially dispersive units. Some, however, are merely resting structures that can tide the fungus over an unfavourable period such as the cold of winter or prolonged drought. To this category belong most rust teliospores, although some are also dispersive, and the oospores of Phycomycetes. Again, zygospores of Mucorales are resting, rather than dispersal, spores, but the part they play in the general biology of these fungi is far from clear.

The great majority of spores have firm cell walls, but the zoospore of water-moulds is naked, although having come to rest it then secretes a wall prior to germination.

Although essentially microscopic, spores of fungi vary greatly in size and shape (Fig. 1.1). Most are, however, spherical or ovoid with a diameter in the range 5–50 μm, but the ascospores of some lichens are nearly visible with the unaided eye. For example, the two-celled ascospore of *Varicellaria microsticta* may be as large as 350 $\times$ 115 μm, nearly as big as the smallest orchid seeds. Many spores are long and thread-like. Thus the septate ascospores of *Cordyceps militaris* may be 500 μm long but only 2 μm wide. In some fungi the spore is a branched structure, a feature particularly characteristic of aquatic Hyphomycetes. Although single spores are microscopic, in the mass they may become conspicuous as in the spore print of a toadstool, or in the smoke-like cloud rising from a puffing *Peziza*, or from a ripe puff-ball (*Lycoperdon* sp.) bombarded by falling raindrops.

Spores vary in colour. Many are transparent and colourless, appearing white in the mass; but they may be yellow, pink, purple, brown, or black,

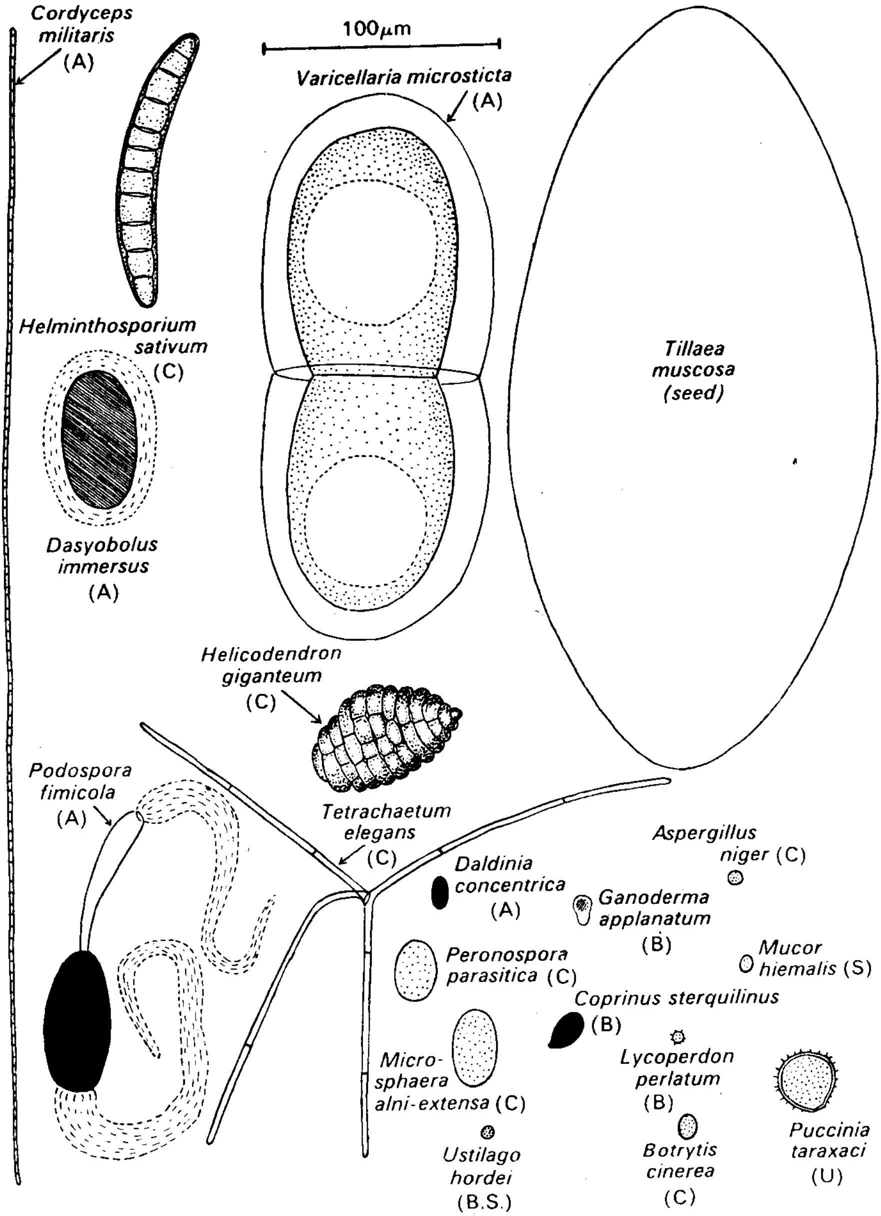


FIG. 1.1. Size of spores. Outline of minute seed of *Tillaea muscosa*, seven exceptionally large fungal spores, and eleven spores of more usual size and form. All drawn to same scale. Type of spore indicated in brackets with each species. (A) ascospore; (B) basidiospore; (B.S.) brand spore; (C) conidium; (U) urediospore; (S) sporangiospore.

and indeed spore colour is an important taxonomic character, particularly in the Agaricales. The colour of spores is due largely to pigmentation in the spore wall, although yellow-orange carotinoid pigments dissolved in oil drops in the cytoplasm may also contribute, particularly in the urediospores of rusts.

Apart from pigmentation, the wall of the spore may vary considerably. It can be thin or thick and either smooth or variously ornamented.

An outstanding feature of most fungi is the enormous spore production. However, on average not more than one spore from each individual succeeds in its reproductive function, since each species is more or less in equilibrium and its numbers, though they may fluctuate from year to year, usually show no steady increase.

Many estimates of spore output have been made, but only a few examples will be given to illustrate its gigantic scale in a wide range of fungi. 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 discharge 30 000 000 000 spores a day, apparently maintaining this output for the whole five months (May to September) of its annual spore-fall period. The small apothecium of *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 a day. In the stinking smut of wheat (*Tilletia caries*) a single diseased grain may contain 12 000 000 brand spores. A colony of blue mould (*Penicillium* sp.) 2·5 cm in diameter may bear 400 000 000 conidia.

An important attribute of a spore from the point of view of dispersal is its retention of the power to germinate. The fact that it may be transported a long distance is of no significance if at the end of its journey it is incapable of growth. The bearing of this on effective dispersal is well illustrated by rusts. On the whole urediospores are very resistant, and being able to survive for a long time in the air, in spite of both dessication and intense insolation, can carry rust infection in a single step to a distance of hundreds of miles. 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 diseased plants. However, all too little is known about the retention of viability in spores during the course of their dispersal.

The great majority of fungi are spread by spores, but some employ other means of dispersal. In the minute agaric *Omphalia flavida*, for example, which causes a leaf-spot of coffee and many other plants in the New World, although fruit-bodies are formed liberating basidiospores, reproduction also occurs by macroscopic gemmae (Fig. 1.2). Each of these appears to be homologous with a pileus, but much smaller. When ripe it becomes loosened from its stipe, is readily blown away, and,