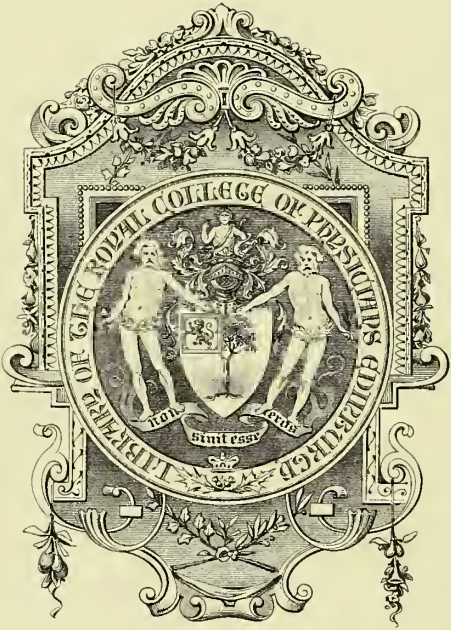
A TEXT-BOOK OF FUNGI

GEORGE MASSEE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TEXT-BOOK OF FUNGI

Text-Book of Fungi

INCLUDING MORPHOLOGY, PHYSIOLOGY, PATHOLOGY, CLASSIFICATION, ETC.

BY

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'EUROPEAN FUNGUS-FLORA'; 'BRITISH
FUNGUS-FLORA,' ETC., ETC.

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TO

SIR WILLIAM T. THISELTON-DYER,

K.C.M.G., C.I.E., LL.D., SC.D., M.A., F.R.S.,

EMERITUS DIRECTOR, ROYAL BOTANIC GARDENS, KEW,

to whom I am greatly indebted for much kindly encouragement in connection with my work, both previous to and during my official tenure at Kew; I have great pleasure in dedicating this attempt to introduce to English students those features which collectively constitute the study of Mycology, as understood at the present day.

GEO. MASSEE.

PREFACE

DURING recent years it may be truly said that our knowledge of Fungi, from morphological, biological, and physiological standpoints respectively, has increased by leaps and bounds. This extended knowledge is reflected in the improved method of classification adopted at the present time, which, in many instances, is no longer solely based on morphological analogies derived from a cursory examination of mature forms, but on the sequence of development and linking up—in many instances—of the various phases included in the life-cycle of a species.

The object of this little book is to serve, in some measure, as an introduction to those comparatively new lines of research, and also to indicate where fuller information may be obtained.

The chapter on 'Biologic Forms' was kindly prepared at my request by Mr. E. S. Salmon, F.L.S., our chief exponent of this subject, to whom I take this opportunity of repeating my best thanks.

I have no particular axe to grind, and in utilising the information culled from various authors, if I have in any sense misconstrued their views, I can truly say that it is owing to my inability to grasp the point, and not to wilfulness.

Finally, to my colleague, Mr. A. D. Cotton, F.L.S., I beg to tender my thanks for assistance in proof-reading, and for valuable suggestions.

GEO. MASSEE.

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I.—MORPHOLOGY, PHYSIOLOGY, BIOLOGY, ETC.

II.—PATHOLOGY

III.—CLASSIFICATION

I.—ANATOMY, BIOLOGY, ETC.

INTRODUCTION

THE study of Fungi from other than a systematic or morphological standpoint may perhaps, without prejudice to earlier botanists, be said to have been initiated by De Bary, whose brilliant researches, continued by his disciples and others more or less directly under their influence, have gradually raised our knowledge respecting these plants to a level with that relating to most other divisions of the Vegetable Kingdom.

Cytology has been prosecuted with marked success; such terms as karyokinesis, implying the presence of nuclear spindle, equatorial plate, chromatin grains, etc.; centrosomes, centrospheres, reduction of chromophores, etc., occur now in every cytological treatise dealing with fungi, whereas a very few years ago, it was only from analogy that such structures could possibly be conceived to exist.

The investigations made in this branch of study are as yet too limited to admit of broad generalisations; nevertheless, what has already been done is not without phylogenetic significance. Its influence on our knowledge respecting the sexuality of fungi is most marked, and appears to furnish incontrovertible evidence in favour of De Bary's view of the existence of true sexuality in the Ascomycetes, as opposed to the idea on this point entertained by Brefeld, who denies sexuality to all groups excepting the Oomycetes and Zygomycetes.

On the other hand, speaking broadly, the sexual mode of reproduction is on the wane in the fungi, and instances are not wanting where, even in allied forms, one species may have sexual organs of functional value, whereas in others these organs are sterile, more or less rudimentary, or absent. It is even possible that sexual reproduction may not be constant in the same species. This gradual degeneration of the sexual process, which commences in the Oomycetes, and, so far as we know, has entirely disappeared in the Basidiomycetes, is probably due to an adaptation to terrestrial conditions. These altered conditions also account for the change from the sporangium containing zoospores in *Peronospora*, into wind-borne conidia.

If we accept as evidence of sexual fertilisation in fungi the fusion of a male and female nucleus derived from more or less specialised cells respectively, to form the first nucleus of a new generation, as is known to occur in the higher plants and in animals, then considerable additions have been made to the number of sexual forms, not only in groups where sexuality was previously known, but also in others where its existence was denied, or conclusive evidence was not forthcoming.

In the Saprolegnieae, according to De Bary, Ward, and Hartog, fertilisation does not occur, the tube of the antheridium not opening into the oosphere, although it adheres to it. Quite recently, however, Trow has demonstrated that in *Achlya debaryana* fertilisation does occur, and probably also in other allied species.

Trow's discovery, however, does not prove that the conclusions arrived at by others are incorrect; as previously stated, in species closely allied, some may still retain a sexual mode of reproduction, others not.

In the Ascomycetes Harper has demonstrated the occurrence of a sexual process in *Sphaerotheca Castagnei*, *Pyronema confluens*, etc.

Finally, Blackman has recently announced the discovery of a sexual mode of reproduction in the Uredineae. This consists in the fusion of two nuclei in certain cells in the Aecidium stage. This, however, does not conform with the definition of sexual reproduction as stated above, and as it occurs at a definite stage in the individual immediately preceding the formation of spores, it may possibly prove to be homologous with the fusion of nuclei noted by Dangeard in the Ascomycetes and the Basidiomycetes.

The last-named author has shown that in the Basidiomycetes, a fusion of two nuclei takes place in the basidium, which is considered as an oospore. In the Ascomycetes a similar fusion of two nuclei occurs at the base of the young ascus. Both instances are considered by Dangeard as examples of true sexual reproduction, who consequently does not admit Harper's statement respecting *Sphaerotheca*. This fusion of nuclei in all cases just precedes the formation of spores.

This view is not generally accepted, one reason being that it occurs in certain species where undoubted sexuality, as defined above, exists, as in *Sphaerotheca*, etc. On the other hand, this fusion of nuclei in the higher groups of fungi appears to fulfil physiologically the functions of true sexual reproduction, inasmuch as invigoration or rejuvenescence is concerned.

Before leaving the subject of sexual reproduction, one more important discovery requires notice. In certain fungi both antheridium and oogonium contain numerous nuclei, sometimes one hundred or more each.

The male nuclei pass into the oogonium, where the male and female nuclei fuse in pairs, the result being a considerable number of nuclei present in the oospore. Stevens has shown that this occurs in certain species of *Cystopus*, belonging to the Phycomycetes, and Harper has demonstrated the same in *Pyronema confluens*, belonging to the Ascomycetes.

The significance of this discovery is not at present obvious, but the fact that in both groups, and even in other species of *Cystopus*, or *Albugo*, as it is termed by American writers, fusion of a single male and female nucleus in the oosphere exists, should at least act as a check on those who are prone to jump to conclusions, and draw up phylogenetic diagrams from a limited amount of evidence.

Concerning affinity and descent much has been done of late years, and if the conclusions arrived at cannot be considered as final, they are at least suggestive, and furnish facts which may eventually go towards substituting homology for analogy.

Brefeld considers the sporangium of the Mucorineae and the asci of the Ascomycetes as homologous organs, and that the latter are derived directly from the former. The recent researches of Léger, Swingle, and Thaxter on the mode of spore formation in the Mucorineae, and of Harper in the Ascomycetes, are considered not to support this view; the marked difference in origin of the spores in sporangia and asci respectively being thought inconceivable in homologous organs. Later research, however, has shown that Harper's definition of an ascospore, founded on a very limited number of observations, is not of general application.

Blackman, in addition to the discovery of sexuality in the aecidium stage of the Uredineae, also announces the presence of a rudimentary trichogyne. This indicates an affinity with the Florideae or red seaweeds, where the trichogyne is still of functional value in fertilisation. A trichogyne is also present in the Ascomycetes, where in some cases, more especially in the members of Thaxter's Laboulbeniaceae, it exercises its function of being the intermediary between the spermatia, or fertilising bodies, and the receptive cell. In other genera, as *Polystigma*, *Poronia*, etc., the trichogyne is functionless or rudimentary.

The occurrence of a trichogyne in such widely separated groups of fungi is considered to suggest more than one independent break away from the algae, which are by almost universal consent considered as the ancestors of the fungi.

It is only justice, however, to state that Brefeld's view of the phylogeny of fungi does not agree with the above statement. According to this author the algae and fungi probably sprang in two distinct lines from the Schizophyta. The lowest group of fungi is the Phycomycetes = Zygomycetes and Oomycetes. From these are descended the Mesomycetes = Hemiasci and Hemibasidii. From these again are derived the Mycomycetes = Ascomycetes and Basidiomycetes.

In the Basidiomycetes and the Uredineae the cells contain a single nucleus during the early stage of their life-history. At a later stage the cells in both groups become binucleate. This is considered by Harper as evidence of phylogenetic affinity between the two groups, a point that had previously been suggested from a morphological standpoint.

Results are as yet too few in number and too contradictory to admit of the formulation of a new scheme of affinity or classification based on cytology. Nevertheless the disciples of this school are very sanguine, and have already done thoroughly good work, much appreciated by all ranks of mycologists. Perhaps it is doubtful whether any real benefit is to be derived from the lengthened theoretical suggestions so conspicuous in cytological papers. Another feature is the contempt for morphological evidence. On this point, in criticising a suggestion of affinity from a morphological standpoint, Davis says: 'Resemblances of form have very little value in such comparisons, and relationships must be traced through agreement in the details of protoplasmic activities.' The same author again, in the same paper, emphasises the above idea as follows: 'Form resemblance must be in complete harmony with cytological conditions to have weight.'

If true, this is very serious indeed. The evidence of descent, supposed to have been obtained from an investigation of fossil plants and animals, etc., but perhaps it is not necessary to dilate on this point.

The discovery by Klebs of the influence of food and surroundings in determining the production of a particular kind of reproductive organ, or of sterility, is of primary importance. He has shown that it is possible to produce at will zoospores, antheridia, or oogonia in certain fungi, depending entirely on the composition, temperature, density, humidity, etc., of the nutrient medium. This discovery has been corroborated and extended by other observers.

Its significance to the systematist, whose specific and even generic characters in certain groups of fungi often depend on the union or separation of the sexes, relative abundance of antheridia, etc., is obvious.

Klebs also considers that there is no inherent law demanding an alternation of generations. Under ordinary circumstances in nature, this is effected mainly through the exhaustion of food in each successive host-plant attacked.

This theory appears to account for the alternation of generations, even in such obligate parasites as the Uredineae. When the aecidiospores of *Puccinia graminis* pass from barberry to wheat, the food in the latter host-plant is not conducive to the formation of aecidiospores, and uredospores are produced. As the wheat plant matures, the composition of the food available for the parasite changes; as a consequence uredospores are no longer formed, but are gradually replaced by teleutospores.

In Australia, *Puccinia graminis* is rampant, but the host-plant of the aecidium stage is absent, consequently the aecidium has dropped out of the cycle of development of the fungus, which, however, still produces uredospores and teleutospores on the one host necessary for this purpose.

Other instances are known where one of the factors in the life-cycle has disappeared without in any way interfering with the continuance of the species.

On the other hand, alternation is sometimes suspended,

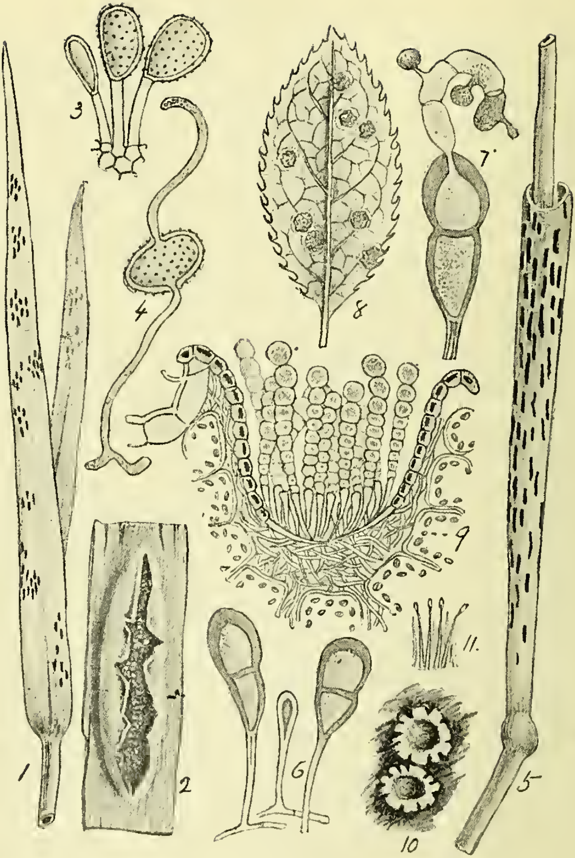

FIG. 1.—*Puccinia graminis*, an heteroecious fungus producing different kinds of spores on different hosts, and on the same host at periods. 1, leaves of wheat plant with pustules of uredospores; 2, a pustule or group of uredospores more highly mag.; 3, uredospores in various stages of development; 4, uredospore germinating; 5, portion of a wheat stem showing pustules of teleutospores; 6, teleutospores in various stages of development; 7, teleutospore germinating; 8, a barberry leaf bearing groups of the aecidium or 'cluster-cup' form of fruit; 9, section of an aecidium containing spores in chains; 10, two aecidia seen from above; 11, sporules from a spermogonium. All figs. mag.

and one stage of the cycle can repeat itself. Dietel has proved experimentally that the aecidium condition of certain species of *Puccinia* and *Uromyces* can be repeated by aecidiospores when sown on a similar host to that on which they were produced, without the intervention of the uredospore or teleutospore stages.

The researches of Klebs are especially significant in connection with 'pure cultures,' which by some are placed on a par with Cæsar's wife. In future, instead of arguing that such cultures prove incontestably the normal sequence of development of a species, we should only go so far as to say that those show what the particular fungus could do under a special sequence of conditions.

The nutrient medium commenced with is constantly changing in composition, density, humidity, etc.; in fact it passes through that sequence of changes which Klebs has indicated necessary to effect radical changes in the behaviour of the fungus under experiment.

As previously stated, cytology has not as yet furnished evidence sufficient for the formulation of a new and improved scheme of classification. New schemes, however, are not lacking. Meyer, on the strength of agreement in possessing 'continuity of protoplasm,' and fusions in vegetative cells, derives all fungi from the Florideae. The Uredineae break away first and recede in a straight line, giving off at an angle the Ustilagineae. These are quickly followed by the Basidiomycetes; the Ascomycetes being the last to start on an independent fungal existence. Why other groups of plants showing continuity of protoplasm even more clearly than fungi are not included in this idea of evolution, is not stated.

Juel has propounded a classification of the Basidiomycetes, turning on the position of the nucleus in the basidium during the stage of spindle formation. If the nucleus is situated about the middle of the basidium, and the axis of the spindle is parallel to the long axis of the basidium, the fungus belongs to the Stichobasidiomycetes. On the other hand, if the nucleus is found to occupy the upper extremity of the basidium, and its spindle is formed at right angles to the long axis of the basidium, the fungus belongs to the Chiastobasidiomycetes.

This scheme will probably not commend itself to all mycologists. It is not always convenient to wait until the nucleus in the basidium is inclined to undergo indirect division, before the section to which a fungus belongs can be determined.

Under present conditions the value of a systematic classification of plants depends entirely on its practicability. Its primary object is to enable us to identify species correctly, and common experience proves that morphological characters are best adapted for this end. Systematic botany thus understood is entirely outside the sphere of cytology, physiology, etc., but, on the other hand, these departments of research are, or should be, dependent on systematic work, to the extent of clearly indicating what particular species has been the object of research. No small number of the controversies and failures in attempting to corroborate the investigations of others have arisen through mistaking one species for another. From the above it will be gathered that what is termed systematic botany is simply useful as a means to an end, whether that end be an endeavour to learn something about the life of a plant, or its certain identification from an economic standpoint. It will thus be seen that the too frequent sneers of cytologists and others are the outcome of ignorance, in expecting from practical systematic botany information that systematists do not profess to furnish.

Side by side with practical systematic botany, but in a separate book, every one would welcome the ideal systematic arrangement of plants based on cytology, morphology, physiology, and everything else that collectively constitutes plant-life; but recent pretentious works attempting a diluted mixture of everything known has resulted in failure. The substance is too diffuse to enable any one to determine a species with certainty, much less to become acquainted with its life-history. A short time ago I endeavoured to trace the origin of the Basidiomycetes from conidial conditions of the Ascomycetes. This idea was founded on morphological agreement in the two groups. In a criticism on this idea Harper says that the occurrence of binucleate cells in the Basidiomycetes and their absence in the Ascomycetes shows that the two groups are widely separated phylogenetically; in the face of such differences, resemblance of outer form and method of spore-formation between conidiophores and basidia must be regarded as superficial and of uncertain value, and as wholly inadequate evidence for the conclusions Massee wishes to draw. Quite recently, while investigating a disease of the cultivated mushroom caused by *Hypomyces perniciosum*, I observed that the cells of a conidial stage of the *Hypomyces*, known as *Mycogone*, were constantly binucleate. In the other conidial form of the *Hypomyces*, called *Verticillium*, the cells are uninucleate.

Woronin has shown that both hyphae and conidia are multinucleate in the conidial form of *Sclerotinia fructigena*, better known as *Monilia fructigena.* In *Sclerotinia aucupariae*, an allied species, the same author shows that the cells of both hyphae and conidia of its conidial form are uninucleate.

This discrepancy in the number of nuclei in the cells of closely allied species does not tend to confirm their value in indicating either affinity or descent. On this point, however, I am not inclined to be dogmatic. The fact remains that binucleate cells are present in the Ascomycetes.

These remarks must not be interpreted as indicating that cytological evidence is not of value; their object is to show the abuse of such evidence. It is obvious in some instances that the paramount importance attached to cytology by its advocates is simply because cytology is the only branch of mycology with which they are familiar.

Specialists in the Uredineae have, during late years, produced good work in the correlation of numerous hitherto isolated forms, the results of which are of great value both from a scientific and an economic standpoint. Heteroecism, however, is not confined to the Uredineae; Woronin has indicated its existence in the Ascomycetes. The ascospores of *Sclerotinia heteroica* are carried by wind on to the young leaves of *Vaccinium uliginosum*, where they form a mycelium which produces conidia a few weeks later. These conidia are again conveyed by wind or insects to the stigmas of *Ledum palustre.* The germ-tubes of several conidia fuse to form a single stout hypha, which passes down the style and forms mycelium in the ovary, that results in the formation of a sclerotium. This sclerotium produces the ascigerous form of fruit the following season. The importance of this discovery turns on the probability that many of the forms included under 'fungi imperfecti' may prove to be phases in the life-cycle of species belonging to the Ascomycetes.

Our knowledge respecting the morphology, correlation of hitherto isolated forms, germination of spores, and general life-history of species included in every group of fungi, has been greatly advanced by the untiring energy of Brefeld, whose investigations are contained in eight volumes, with numerous beautifully executed, if somewhat crowded plates.

No student of fungi can afford to ignore the many investigations by Marshall Ward, which deal mainly with biological and morphological aspects of the subject. Apart from the flood of new light thrown on each subject investigated, these studies are masterly examples of careful and detailed methods and sound reasoning, the outcome of extensive experience. Among other studies by this author may be enumerated: 'A Lily Disease,' dealing with the life-history of a parasitic species of *Botrytis*; 'Disease in Plants'; the predisposition and immunity of the host, and relations between host and parasite; also the biology of *Puccinia dispersa* and its peculiar parasitism on various species of *Bromus*.

Salmon has worked continuously at the Erysipheae for a number of years, with the result that we now know more of this group from a biological, morphological, and systematic standpoint respectively, than of any other family included in the Ascomycetes.

The last-mentioned author has also devoted much attention to the origin and significance of 'biological forms,' or, as they are sometimes termed, 'biological species.' These terms are applied to certain parasitic fungi, when races of a species are respectively confined to a single, or at most a few closely allied host-plants, such hosts not being interchangeable between the different biologic forms. This discovery, due to the investigation of Eriksson, is of primary importance in its bearing on plant diseases due to fungi.

Cooke has furnished us with the most detailed account respecting the geographical distribution of fungi.

The value of the stupendous work entitled *Sylloge Fungorum*, compiled by Saccardo, cannot be overestimated. It contains a diagnosis of every known species, accompanied by references to literature, figures, etc., also habitat, hosts on which the fungus is parasitic, and geographical distribution. The somewhat uneven nature of the work is in no sense due to the compiler, whose primary object was to collect into one work all original diagnoses, some of which are admittedly too brief and inexact to enable any one to recognise the fungus intended. In numerous instances, however, Saccardo has given emended or modern descriptions of species described by the pioneers of mycology. Eighteen volumes have already appeared, and supplementary volumes are still issued as occasion demands, containing all new species described up to date.

Up to the present this work contains descriptions of just over 55,000 species, but it is certain that this far exceeds the actual number of distinct species, and as the work of monographing the various families proceeds it will be found that half the above number will be much nearer the correct estimate. Saccardo has kept up all the form-genera as entities, *Aecidium*, *Uredo*, *Peridermium*, etc., in addition to the myriads of forms included under the Hyphomycetes, Melanconieae, etc., all of which are suspected of being phases in the life-cycle of higher forms. This mode of procedure is, however, perfectly correct from Saccardo's standpoint, for although the groups enumerated are suspected of being only phases in the life of other fungi, this has been only demonstrated in comparatively few instances.

Until such evidence is forthcoming it is very important that all such should be described and named.

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A full bibliography of subjects mentioned in this chapter is not given, as most are treated in greater detail in following chapters.

THE CELL

The cell-wall in fungi presents many modifications of structure and composition. In the vegetative portions the walls remain very thin, as is also the case with the portion concerned with reproduction in the Agarics and many other short-lived species. On the other hand, in many perennial forms, as *Fomes*, *Daedalea*, etc., the walls become much thickened and frequently form a mass as hard and durable as wood. Such thick walls often show stratification, and are frequently coloured, the colouring matter either permeating the entire thickness of the wall, or being confined to certain layers.

A second type of structure presented by the cell-wall occurs in the members of the family of fungi called Tremellineae, also in the cells forming the cuticle in many Agarics, and elsewhere. The peculiarity consists in the outer layer of the cell-wall becoming resolved into a soft, mucilaginous mass, or in many of the Tremellineae the great bulk of the wall behaves in this manner; hence in a section the lumens of the cells, containing granular matter, resemble complete cells enclosed in a dense, colourless mass of gelatinous matter.

Fungi possessing this structure are soft, pliant, and more or less gelatinous when growing; becoming hard, horny, and much contracted when dry, and assume their original appearance when moistened. Among Agarics many species of *Cortinarius* present this peculiarity, the mucilage being produced in such abundance that it actually drips from the cap and stem. In *Mycena rorida* and *M. epipterygia* the stem is covered with dripping gluten derived from deliquescence of the external layer of the cell-walls.

The cell-wall in some instances consists of cellulose, as shown by Wager in the case of *Cystopus candidus*; but in the majority of instances the insolubility of the wall in an ammoniacal solution of cupric hydrate, and the absence of a blue colouration when treated with iodine and sulphuric acid or with Schulze's solution, prove that the wall does not consist of pure cellulose. For this reason

FIG. 2.—*Tremella frondosa.* Half nat. size. (After A. Clarke.)

De Bary suggested the name fungus-cellulose, at the same time remarking that it remained undecided whether such peculiar properties were not due to some foreign deposits in the cell-wall, or to some other causes.

It has been shown by Wisselingh that as a rule the cell-walls do not consist of a special form of cellulose, or fungus-cellulose, but contain chitin, similar to that so frequently met with in the animal kingdom. The test for this substance is as follows. Hyphae are put into a sealed tube in 80 per cent. of hydrate of potash, and heated for two hours to 160 C.; and afterwards placed in 90 per cent. alcohol. On the addition of a solution of iodine and dilute sulphuric acid the characteristic plum-pink colour of chitin is seen.

Pits are frequently present in the cell-wall. In the capillitium threads of many species of *Lycoperdon*, the lateral wall shows minute pits irregularly scattered. In the case of superposed cells forming long strands, as in the stipes of Agarics, the conidiophores of various moulds, etc., the transverse walls are perforated by a minute central pit, thus admitting of continuity of protoplasm, as in the red seaweeds or Florideae. Poirault has stated that continuity of protoplasm is also present in lichens, the protoplasm passing through a minute pit in the centre of the wall. Continuity of protoplasm is, however, most evident in the Laboulbeniaceae.

The most highly differentiated pits that I have observed occurred in the blood-red sclerotium of an orange-coloured Hyphomycete called *Rhinotrichum aureum*. These pits closely resemble in general appearance and structure the bordered pits met with in the Coniferae.

The protoplasm usually occupies the whole of the cavity in young cells, and generally presents a granular appearance. In full-grown cells it becomes vacuolate, and finally one or several large sap-cavities appear, the protoplasm forming a thin layer closely appressed to the inner surface of the cell-wall—the cytoplasm. From this peripheral layer of protoplasm thin strands or plates cross the cell from one side to another. The turgidity of the cell, and the fact that the protoplasm lies close to the inner surface of the cell-wall, is due to the presence of the cell-sap, which, according to the modern theory of solutions, explains that substances in solution in water act like gases, and strive to fly outwards or away from each other.

Movements of protoplasm can be distinctly seen in hanging-drop cultures, and according to Ternetz are neither a circulation nor rotation, but a streaming. The current passes easily through the cell-walls, or possibly through a central pore, and always maintains the same direction. Its purpose appears to be the counteraction of differences of turgor in different parts of the filament.

On the other hand, Arthur observed that in certain Mucors the currents of protoplasm are irregular and change their direction, and are due to osmotic absorption of water at some points of a filament, and to extravasation of water at other points.

Vacuoles are not simple cavities in the protoplasm, but have a definite membrane according to Went, whose statement is supported by other observers. De Vries has shown by plasmolysis that the wall of the vacuole is an osmotic membrane.

The nucleus, as described by Wager in the basidia of *Agaricus muscarius* and in *A. stercorarius*, agrees in structure with that present in higher plants; it possesses a nuclear membrane, nucleolous, and nuclear network made up of a thread coiled into a somewhat loose knot.

The division of the nucleus is distinctly karyokinetic or indirect, and again corresponds in all essentials with that observed in higher plants and animals. A suggestion of the presence of centrospheres was noted at each end of the nuclear spindle in the species mentioned above, but at a later date these bodies were clearly observed by Wager during the division of the nucleus in *Agaricus galericulatus*. Gjurasin has also described the presence of radiating striae probably corresponding to centrosomes, at the poles of the

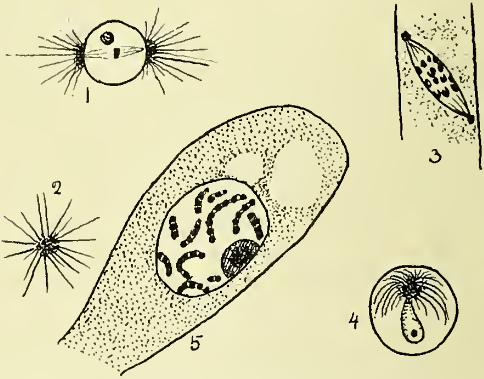

FIG. 3.—1, equatorial plate stage of first spindle. A nucleolus is present, as are also centrosomes and astral rays at poles of spindle; from ascus of *Hydnobolites*. 2, polar view, showing centrosome and astral rays; from nucleus in ascus of *Hydnobolites*. 3, first spindle after cleavage of chromosomes, minute centrosomes are present at the poles of the spindle; from ascus of *Neottiella albocincta*. 4, elongated nucleus in young spore of *Hydnobolites*, showing a nucleolus, centrosome, and astral rays. 5, basidium of *Amanita muscaria* with nucleus, in which the nuclear thread, or threads, is broken up into a number of short, slightly curved rods. The protoplasm of the basidium shows two large vacuoles. (Figs. 1-4 after Faull, fig. 5 after Wager.) All highly mag.

nuclear spindle in *Peziza vesiculosa*, an Ascomycete. The presence of centrospheres in the cells of animals has long been known. In plants they have been observed chiefly in cells concerned with reproduction, where they perform an important function, inasmuch as the division of the nucleus is determined by their influence in causing the separation of the chromatin segments of a single nucleus into two groups, each of which eventually becomes a nucleus. This is effected by the two centrosomes, located at opposite ends of the nucleus, repelling each other; hence these bodies have been termed kinetic centres or attraction spheres. In a typical centrosphere there is a central differentiated portion called the centrosome, and such structures have been observed in connection with the division of nuclei in the oosphere of *Cystopus bliti* by Stevens. This author also states that in the species mentioned above, the sexual nuclei differ in form, the male being elongated and the female spherical.

Chromosomes are formed by the fusion of the chromatin-granules in the thread forming the nuclear network. A reduction of chromosomes during nuclear division has been observed by Stevens.

Guilliermond has demonstrated that Dangeard's generalisation, that the Ascomycetes have constantly four chromosomes, is not correct. He observed eight in *Peziza cerea* and in *P. vesiculosa*, twelve in *P. cotinus*, and sixteen in *P. rutilans*. Trow points out that in *Achlya de Baryana*, the reduction in the number of chromosomes, from eight to four, takes place in the gameto-genesis, as in most animals, and not in sporo-genesis, as in most plants.

During the stage of nuclear division in the oosphere of *Cystopus candidus*, Wager observed the appearance of a central homogeneous body in the cytoplasm, apparently formed by the gradual condensation of a mass of granular cytoplasm. The function of this organ appears to be that of bringing the sexual nuclei together. It has since been observed in the oosphere of other species of *Cystopus*, also in *Peronospora*. Stevens considers that this organ may be of a dynamic nature, and proposes the name coenocentrum. After fertilisation this structure disappears.

In addition to the complex mode of nuclear division described above, nuclei present in vegetative mycelium sometimes divide in a simpler manner, without any formation of a nuclear spindle, etc. Such a method is known as direct division, or fragmentation. By this method several nuclei are often produced in a single cell, as described by Raciborski in certain cells of *Basidiobolus*.

Fatty matter or oils are abundant in the cells, and during active growth are in the form of myriads of very minute particles, giving to the protoplasm a turbid or granular appearance. During the resting-stage in spores, sclerotia, hybernating mycelium, etc., these minute particles often collect into large drops, which are either colourless, or sometimes brilliantly coloured. In many of the Discomycetes and others, there are constantly two such oil-guttules—at one time called nuclei by systematists —in each spore. In some species, but not all, the oil drops assume a brilliant red colour when treated with a solution of alcannin.

Glycogen was shown by Errera to be abundant in the cells of fungi, more especially in the asci of the Discomycetes and the Tuberaceae. It is intimately mixed with the protoplasm, which in consequence appears very refringent. It assumes a reddish-brown or coppery colour when treated with iodine. It is a hydro-carbon compound, and is considered by Errera as reserve material of equal value to fungi as starch is to chlorophyll producing plants.

Fibrosin bodies is the name given by Zopf to certain minute discoid or cone-shaped bodies present in the conidia of *Podosphaera oxyacanthae*. These again are hydro-carbon reserve material, and are insoluble except in concentrated mineral acids.

Volutin is the name given by Meyer to certain minute spherical bodies met with mostly in the cytoplasm, where they are of constant occurrence in many families, and are also met with in considerable abundance in most groups of plants. This reserve material is considered to be of special importance, for in addition to the C, H, and O of fats and carbon-hydrates, it also contains N and P atoms in its composition. The most general test for its presence is a deep blue colour on the addition of one part of Ehrlich's methylene blue in ten parts of water, added to one part of concentrated sulphuric acid in ninety-nine parts of water.

Oxalate of lime is an abundant product, although but rarely occurring in cells. On the surface of cells it is of common occurrence, as on the pilei of *Agarics*, *Coprinus micaceus*, *Psilocybe atomata*, etc. The sporangial walls of many species of *Mucor* are also incrusted with a layer of very minute crystals. Under the form of minute needles or amorphous particles, it is not uncommon on or in the substance of the walls of young vegetative hyphae. In vegetative hyphae of *Ithyphallus impudicus*, certain large globose or flask-shaped vesicular cells are almost filled with a radiately crystalline mass of oxalate of lime.

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ANATOMY OF FUNGI

The spore on germination usually gives origin to a cylindrical outgrowth or germ-tube, which by continued apical growth and the formation of lateral branches produces a more complicated structure called a hypha. The hyphae collectively constituting the vegetative portion of the fungus, so long as they remain free from each other, that is, not compacted together to form solid masses or cord-like bodies, constitute the mycelium, popularly known as spawn. In some fungi belonging to the Phycomycetes the hyphal system consists of one continuous tube, or becomes cut up into cells by the formation of cross-walls or septa previous to the formation of fruit. In the majority of fungi, however, the hypha develops as a string of cells owing to the continuous formation of septa just behind the apex. In some instances intercalary septa are formed at a later period in portions of hyphae remote from the growing point.

A peculiar feature common in most groups of fungi, excepting the Phycomycetes, is the coalescence at various points of independent hyphae. When spores germinate in a hanging drop, the different germ-tubes that come in contact fuse together, the walls of both hyphae disappear at the point of contact, and the cavities of the two tubes become continuous. In some instances an irregular network of hyphae, resulting from numerous fusions, is formed. In other instances where two hyphae run parallel to each other, but at some distance apart, a lateral branch from one hypha grows out until its point comes in contact with the other hypha, when fusion takes place, forming an

H-shaped structure. Such unions are often abundant where several hyphae run more or less parallel to each other. Such coalescence of germ-tubes is very pronounced in the case of germinating secondary spores or pro-mycelial spore in the Uredinaceae and the Ustilaginaceae, where it

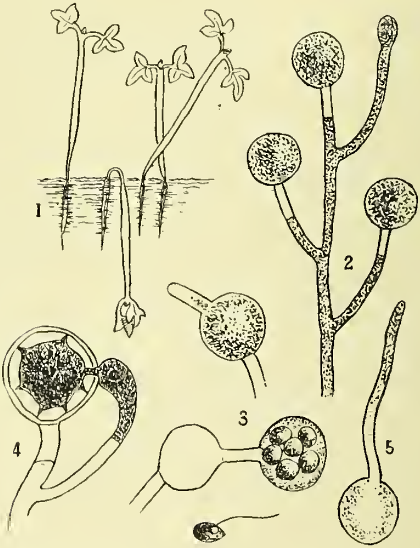

FIG. 4.—*Pythium debaryanum*, a fungus having aseptate mycelium during its vegetative condition. Septa appear when the fruit is produced by which the latter is cut off from the remainder of the mycelium. 1, seedlings of cress (*Lepidium sativum*) attacked by the fungus; 2, mycelium bearing conidia at the tips of the branches; 3, sporangia of different ages, also a free zoospore; 4, an oosphere, with an antheridium or male organ, which has pierced the wall of the oosphere and inserted a fertilising tube (after this blending of the contents of oosphere and antheridium, the oosphere becomes surrounded by a thick wall, and becomes the oospore, or sexually formed resting-spore); 5, a germinating conidium. All figs., except 1, mag.

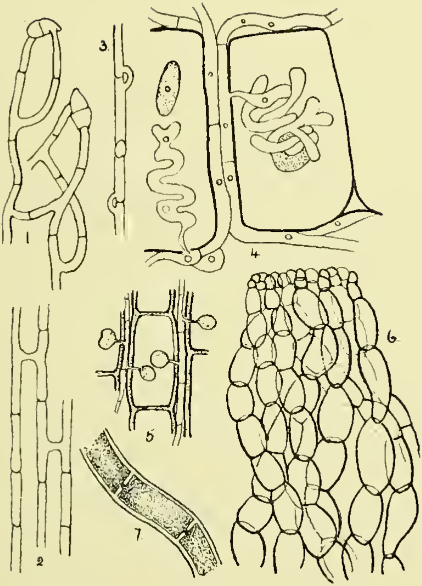

FIG. 5.—1. Germinating spores of *Trichothecium roseum*, showing anastomosing hyphae; 2, anastomosing hyphae of *Mycena galericulata*, forming H connections; 3, hypha of *Agaricus muscarius*, showing clamp-connections; 4, intercellular mycelium of *Puccinia violae* sending haustoria into the cells of a violet leaf; 5, haustoria of *Gymnosporangium juniperinum* in cells of juniper; 6, section through a portion of the outside part of the ascospore of *Peziza vesiculosa*, showing false tissue composed of more or less parallel rows of hyphae. 7, portion of sporongiophore of *Botrytes cinerea*, showing continuity of protoplasm through a central pore in the transverse septa. Fig. 4 after Sappin-Trouffy. All highly mag.

is said by Dangeard to compensate for the absence of the mingling of protoplasm in his supposed sexual process.

Ward investigated this phenomenon in detail in the hyphae of a species of *Botrytis* in hanging-drop cultures. The fact that a hypha could be deflected through a right angle to fuse with another hypha suggested the idea that some attraction is exercised. Hyphae do not always fuse when they cross each other, and to bring about the necessary attraction it is assumed that the hyphae must contain a ferment substance in the necessary quantity or condition of action, or both, before two hyphae can fuse together. Another peculiar method of coalescence characteristic of the Basidiomycetes, but not strictly confined to this group, is known as clamp-connections. This arrangement is only met with where the hyphae are broken up into cells by transverse septa. A protuberance forms laterally on the wall of a hypha, close to a transverse septum, and increases in length until its apex comes in contact with the adjoining cell of the hypha situated on the other side of the septum; the point of the outgrowth and also that of the wall it touches are absorbed; thus open communication by means of this neck is set up between two cells of a hypha that were originally separated by a transverse wall. At a later stage one or both openings from the cells of the hypha communicating with the lateral clamp are again closed. These clamp-connections are arranged in a spiral manner around the hypha, each one being a little to the right or left of the one below or above it.

The combination of hyphae to form a tissue is effected by the intertwining of the component threads, and not by cell-division as in the higher plants, where successive septae are arranged in two or three directions of space;

hence fungus tissues are spoken of as false tissues. In many instances, as in the stipes of Agarics, the interweaving of the hyphae is very evident in a section, the general texture is loose, and there are numerous air-spaces. In other cases the tissue is hard and compact, and without air-spaces, as in sclerotia, the cuticle of the pileus in some species of *Polyporus*, etc. Elsewhere as in the perithecia or fruits of the Sphaeriaceae, and the tissue of the sporophore of some of the Discomycetes, thin sections cut in whatever direction show isodiametric cells resembling true parenchymatous tissue, but when such structures are examined in a very early stage of development, their origin from independent hyphae is obvious.

The tissues of fungi are grouped as follows by Istvanffi :—

1. *Merismatic System.*—Tissues corresponding to the meristem of higher plants are rarely clearly differentiated. The tips of many rhizomorphs bear a resemblance to the tips of true roots, the mucilaginous sheath in the rhizomorph of *Agaricus melleus* corresponding to the root-cap. Zones of growth are also present in the pileus of *Agaricus*, *Polyporus*, *Stereum*, etc.

2. *Protective System.*—Under this heading come the various forms of cuticle, in some Agarics consisting of a layer formed of more or less parallel hyphae, which are sometimes cemented together by a substance derived from the deliquescence of the outer layer of the hyphal walls; in other instances, as in various species of *Polyporus*, the cuticle becomes pseudoparenchymatous and exceedingly hard. Cystidia, when mineralised, prevent the spores from being removed by slugs, snails, etc. Thick coat of oospores and various resting-spores. Mechanical arrangements for retaining the general form of the fungus consist in the

elasticity of the cell-wall and turgidity in unicellular forms, whereas in multicellular species there are such factors as transverse septa, thickening of the cell-walls, and in some of the higher forms of *Polyporus* there is a specialised

FIG. 6.—*Tilletia tritici*, a fungus showing secondary spores fusing in pairs. 1, ear of wheat attacked by the fungus; 2, a spore; 3, 4, spores germinating and producing a germ-tube bearing a cluster of secondary spores at the tip; 5, two secondary spores that have conjugated or joined by a transverse outgrowth; one of the secondary spores has produced a sporidiolum. All, except fig. 1, mag.

system which remains as a skeleton, after all the other parts of the fungus have decayed or been removed by beetles, mites, etc.

3. *Conducting System.*—Plastic substances, as latex and oil that are used up during the fruiting period, are contained in inflated cells or more frequently in differentiated laticiferous hyphae.

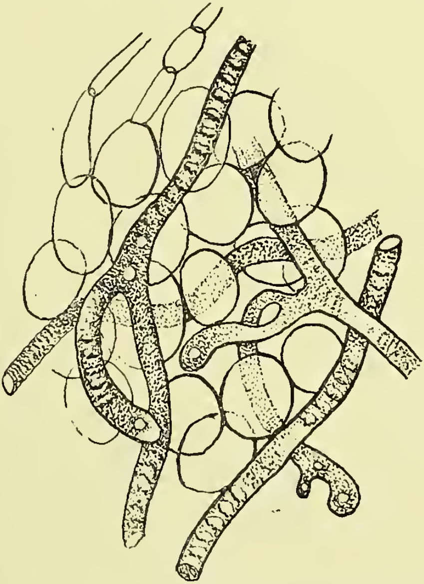

FIG. 7.—Laticiferous hyphae mixed with vesicular hyphae in gill of *Russula rubra*. Highly mag.

These specialised conducting tubes originate as lateral outgrowths from ordinary hyphae, are at first multinucleate and transeversely septate, although the septa eventually disappear. In some Agarics, more especially in the genus *Lactarius*, the laticiferous tubes are variously branched, and anastomose freely, and form a differentiated tissue in the stem, but are also present in every part of the fungus. In this genus the quantity of latex present is so abundant that it escapes in the form of drops when a slight wound is made in the flesh. The storage of reserve food is met with most abundantly in sclerotia, but not infrequently certain of the cells in single hyphae become much swollen and thick-walled, and contain reserve food. Such swollen intercalary or terminal cells have more than once been described as the oospores of *Saprolegnia* and allied forms, when met with in sections of fossil wood.

4. *Reproductive System.* — Includes those portions directly concerned with the production of reproductive bodies, sporophores, conidiophores, oospores, spores, conidia, zoospores, etc.

In the majority of fungi the entire mass of vegetative hyphae or mycelium must be considered as nutritive in function, as when the mycelium spreads in humus, dead wood, etc., and even in the case of those parasites where the hyphae are intercellular, or run between the cells of the host-plant. On the other hand, in many parasites certain portions only of the mass of vegetative hyphae are concerned with the act of nutrition. In the Perisporiaceae, which are unique in having the vegetative mycelium superficial, and forming a more or less evident weft on the surface of the host-plant, certain portions of hyphae that are in direct contact with the surface of a leaf produce a very delicate lateral branch, which pierces the epidermis of the host-plant, and enters an epidermal cell. Inside the cell the slender branch of mycelium, called the neck, swells into a more or less globose or slightly lobed body or haustorium, which contains a nucleus. In *Erysiphe* *communis* and others an ingrowth of the inner wall of the host-plant forms a sheath round the neck of the haustorium for some distance, and the haustorium itself is surrounded

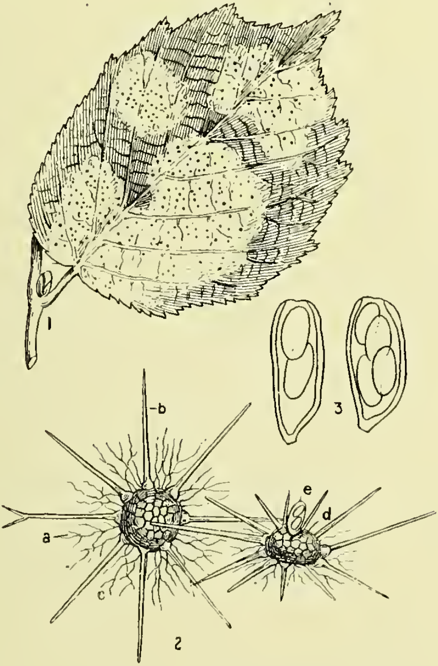

FIG. 8.—*Phyllactinia suffulta*, a fungus having superficial mycelium which grows on the surface of the host-plant. 1, a hazel leaf partly covered with the white mycelium of the fungus; 2, fruit of the fungus furnished with spine-like, projecting appendages; 3, asci containing spores. All, except fig. 1, mag.

by a vesicular membrane which separates it from the protoplasm in the cell of the host. The haustorium is the absorbing organ which supplies the fungus with food, at the expense of the cell of the host in which it is located. The nucleus of the host-cell is usually not interfered with. In the majority of the Erysipheae the haustoria are of the type described above; in some instances, however, the haustoria show indications of a type of structure met with in other groups. In *Erysiphe graminis* the haustoria branch into a number of finger-like outgrowths. In *Phyllactinia*, another genus belonging to the Erysipheae, branches of the superficial hyphae enter the leaf through stomata, wander for a short distance in the intercellular spaces of the leaf, and send off haustoria into the cells. Sappin-Trouffy has shown that in the Uredineae, haustoria are as well developed as in the Ustilagineae and the Peronosporeae, the nucleus of the host-cell being attacked and deformed.

In the Peronosporeae intercellular mycelium is abundant in the tissues attacked; usually leaves, and haustoria penetrate the cells by a narrow neck, which forms inside the cell several more or less elongated, multinucleate branches. In the mycorrhiza of orchids and other plants, the haustoria usually grow directly towards the nucleus on entering a cell, and envelop it in a dense hyphal coil.

In some instances the fungus is fixed to the substratum by means of many independent fascicles of hyphae which are spoken of as rhizoids; this arrangement is very evident in the genus *Rhizina*, also in Lichens, as the species of *Peltigera*. Such rhizoids perform the dual function of organs of nutrition and of mechanically fixing the plant to its nutrient body.

FIG. 9.—*Armillaria mellea*, showing the sporophore or reproductive portion of the fungus, which consists of pileus or cap, bearing the gills which produce the spores, on its lower surface; stem; and secondary veil, a membrane which extends from the stem to the margin of the pileus, thus protecting the gills when young; at a later stage this membrane splits and breaks away from the pileus, shrinks and forms a ring or collar round the stem. The vegetative portion of the fungus is buried in the ground. Half nat. size.

Excepting the Perisporieae the vegetative portion of the fungus is immersed in the substratum on which the plant is growing, and the portion growing in the air is entirely devoted either directly or indirectly to reproduction, and is called the sporophore. Thus in the common mushroom (*Agaricus campestris*), the stem, cap, and gills bearing the spores collectively constitute the sporophore, whereas the mycelium or spawn hidden away in the ground represents the nutritive portion of the fungus. As an exception to the above general statement, it may be pointed out that in some of the primitive types of fungi belonging to the Phycomycetes, as species of *Saprolegnia*, etc., the vegetative and reproductive portions are not sharply differentiated, and both are immersed in the substratum, which on decay liberates the spores. Such species are aquatic in habit, and spore distribution is effected by water, but when fungi became terrestrial in habit and dependent on wind for spore dispersion, then the sporophore became superficial; in those instances where the fruit is immersed in the matrix, as in species of *Sphaeria*, *Valsa*, etc., some provision is made, either in the form of a tubular neck to the fruit, reaching above the surface of the matrix, or the rupture of the latter, for liberating the spores in the air at maturity.

As would be expected in such an enormous assemblage of species, the variety of form and relative complexity of structure of the sporophore is manifold. In some primitive forms as the Chytridiaceae, where the mycelium is almost obsolete, the conception of a sporophore is not possible, and the same may be said of the oospores of the Peronosporeae, etc., that are borne on short lateral branches, or intercalary—that is, produced from certain cells in a length of hypha which runs in the tissues of the host.

The primary object of a sporophore is that of facilitating the dispersal of spores by wind or other agents, hence it is only present in a differentiated form when it rises above the substratum.

FIG. 10.—*Helminthosporium turcicum*, a fungus with simple conidiophores growing in clusters. Each conidiophore bears a single many-celled conidium at its tip. 1, portion of a leaf of maize showing a large dark blotch formed by the fungus; 2, conidiophores bearing conidia. Fig. 1, nat. size; fig. 2, mag.

It is customary where a fungus produces two or more distinct forms of reproductive bodies, as in species of

Peronospora, *Cordyceps*, etc., to speak of the specialised structure bearing the conidia or asexual reproductive bodies as the conidiophore, and the one bearing the higher or sexual form of fruit as the sporophore. This method, however, is not consistently followed, as in the Basidiomycetes, where no sexual form of reproduction is present, the only reproductive bodies being of asexual origin, and hence should be called conidia; these are, however, as a matter of fact always spoken of as spores, and the structure producing them is called a sporophore. On the other hand, in such genera as *Xylaria*, *Thamnomyces*, etc., the same specialised structure or sporophore first produces conidia, and afterwards the higher or ascigerous form of fruit.

In *Mucor mucedo* the conidiophore consists of a single erect non-septate hypha, bearing a single sporangium at its apex. In allied species the conidiophore bears a few branches, each terminated by a sporangium containing conidia, usually spoken of as spores.

In a slightly more complex form the conidiophore commences as a single upright hypha, which becomes more or less branched above, the branches ending in a short pair of branchlets, each bearing a conidium; this type is illustrated by various species of *Peronospora* and allied forms. Further complexity is introduced where the lower or sterile portion of the conidiophore is composed of a loose fascicle of hyphae, the tips of which become free from each other and more or less spreading above, forming a head, the tip of each hypha bearing one, or a chain of conidia, as in *Stysanus*, *Isaria*, etc. In *Hypoxylon*, *Cordyceps*, *Daldinia*, etc., the sporophore becomes stout and fleshy, and is composed of numerous hyphae compacted into a dense, firm substance, which in some cases first bear conidia on its surface, and afterwards the ascigerous

FIG. 11.—*Peronospora schleideni*, a fungus with a much-branched conidiophore. 1, a conidiophore that has emerged into the air through a stoma in an onion leaf; 2, free conidia; 3, oospore or resting-spore. All mag.

form of fruit, the individual perithecia being immersed in the peripheral portion of the sporophore, with an opening to the exterior for the escape of the spores. This type of

FIG. 12.—*Plowrightia morbosa*, a fungus with a large, irregularly shaped black stroma in the substance of which numerous perithecia containing spores are immersed. 1, portion of a branch of a plum-tree bearing a stroma of the fungus covered with conidia; 2, portion of a branch with a stroma of older date and bearing perithecia; 3, conidiophores with conidia near the tip; 4, ascus containing eight ascospores: by its side is a paraphysis. Figs. 1 and 2, half nat. size; the others mag.

sporophore is often termed a stroma, the conception of which is a more or less fleshy, erect, or broadly effused sporophore, as in *Hypoxylon*, having numerous perithecia or flask-shaped fruit-cases containing asci embedded in its substance. A stroma may be considered as a compound fruit in the same sense as the mulberry and pine-apple are spoken of as compound fruits; each perithecium enclosed in the stroma being an entity, in the sense of originating from an independent sexual act—that is, if the sexual organs are of functional value at the present day.

The greatest variety in form and structure presented by the sporophore is met with in the Basidiomycetes. In the simpler forms, as *Corticium*, it forms a broadly effused crust firmly attached to the substratum at every point, and covered everywhere on the upper free surface with the hymenium or specialised spore-bearing surface. Such a sporophore is described as being resupinate or adnate. In the genus *Stereum* we get a first glimpse of the structure, which, after considerable evolution in the various families of the Basidiomycetes, results in the parasol-shaped structure met with in Agarics or toadstools. In some species of *Stereum* the whole of the sporophore is resupinate and everywhere firmly attached to the substratum, as in *Corticium*. This occurs when the fungus is growing on the upper surface of wood lying on the ground—that is, where the surface of the fungus is parallel with the ground. On the other hand, when the same species is growing on a vertical log, it commences as a resupinate patch, but not infrequently the edge of the sporophore farthest removed from the ground becomes free and grows out more or less at right angles to the log. Here we have the first indication of the inferior hymenium

—that is, pointing to the ground, and also the most primitive attempt at protection of the hymenium against rain, dust,

FIG. 13.—*Stereum hirsutum*, a fungus having a sporophore which is partly adnate to, or lying flat and attached to the matrix, whereas the upper portion of the sporophore is free from the matrix, and grows at right angles to it. The hymenium or spore-bearing portion is on the under side of the free portion; the upper side is sterile and protective. 1, fungus growing on a piece of dead wood; 2, section of same; 3, basidia, each bearing four spores. Figs. 1 and 2, nat. size; fig. 3, mag.

etc. The upper or sterile free portion of the sporophore is called the pileus by systematists, and when it originates as above, fixed by a more or less broad base, and growing at right angles to the matrix, the sporophore is said to be dimidiate. This type of sporophore is very commonly seen in species belonging to the Thelephoraceae and the Polyporaceae, when growing on the vertical surface of trunks, posts, etc. A further approach to the truly central stem, as seen in most Agarics, is brought about by the gradual narrowing of the point of attachment of the sporophore, at the point where it becomes free from the matrix or support on which it is growing. When this point of attachment is much reduced, the sporophore grows out as a more or less circular or fan-shaped sporophore, supported by a short, narrow, stem-like base, and is described as flabellate. If we imagine the two free margins of the sporophore nearest the stem adhering together, we get the first suggestion of a central stem supporting a pileus, sterile and protective on the upper surface, and bearing the hymenium on its under surface, and pointing towards the ground. The upward growth of the stem, and the downward growth of the gills in Agarics, the spines in *Hydnum*, etc., are said to be due to negative and positive geotropism respectively.

In Agarics the margin of the pileus is strongly incurved when young, so that it is in contact with the stem, and the extreme edge is also often inrolled on itself. This is stated by De Bary to be due to epinasty, or the more vigorous growth of its upper surface than that of the lower. At a later stage of growth the pileus gradually expands and changes its original bell-shape for that of an expanded umbrella, or may become plane with the edge more or less upturned. This is due to hyponasty, or the more rapid growth of the under than the upper surface of the pileus.

In the perennial fungi, as various species of *Polyporus*, increase in size takes place by the formation of a new

FIG. 14.—*Fomes fomentarius*, a large perennial fungus having a hard, woody sporophore. The upper surface is sterile, the hymenium being situated on the flattened under surface. A new hymenial layer is formed each season upon the previously existing one. The different layers of hymenial tissue are indicated by lines as shown in the section. Each layer extends a little beyond the previous one, hence the hymenium increases in area each year. The ridges on the surface roughly correspond to the number of hymenial layers. One quarter nat. size.

hymenial layer on the surface of the preceding one. The hyphae forming this new hymenium also grow round the margin of the hymenium and edge of the sporophore; thus the hymenium of each succeeding year occupies a greater area than the previous one it is built upon. Owing to this successive formation of one hymenium upon another, a section of the fungus shows a stratified appearance, and the age of the fungus can be determined by counting the number of superposed layers of tubes, assuming that a layer had been formed each year, which takes place under normal conditions. In like manner the addition each year to the margin often forms a corresponding ridge on the sterile upper surface of the pileus, and the succession of ridges and differently coloured zones on the surface of the pileus of perennial species are explained in this manner.

The spores or reproductive bodies in the broader sense, including conidia, present a very varied sequence of general form and structure. In all the Basidiomycetes the spores are one-celled or continuous; this is also true of large numbers of conidia. In the Protobasidiomycetes the spores often consist of more than one cell, or, as expressed by systematists, the spore is one-septate, or consisting of two cells; when three-septate the spore consists of four cells. The reason for this is, all spores are at first one-celled; then, if the spore is of an elongated form, a transverse wall or septum first appears dividing the cell into two equal portions, or cells; each cell then undergoes division in a similar manner, the result being a three-septate spore, or a four-celled spore, whichever term is favoured by the systematist. By the continued formation of transverse walls a multiseptate or multicellular spore or conidium is formed. In many instances, more especially in the case of spores produced in asci, septa are formed at right angles to

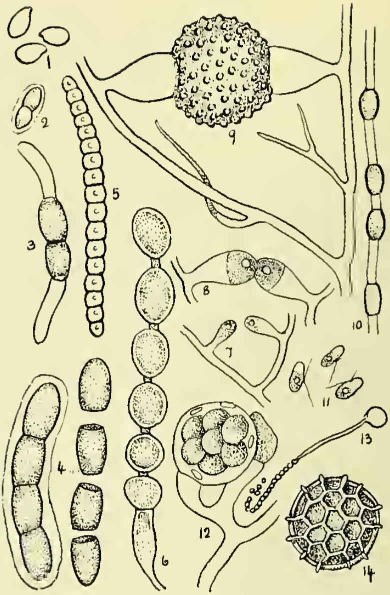

FIG. 15.—1, basidiospore of *Collybia radicata*. 2, ascospore of *Delitschia maravica*, 1-septate, and surrounded by a colourless gelatinous coat. 3, ascospore of *Delitschia insignis*, 1-septate, and with a hyaline appendage at each end. 4, ascospore of *Sporormia ovina*, 3-septate, and surrounded by a hyaline gelatinous coat. In the right-hand figure the gelatinous sheath has disappeared, and the spore has broken up into four component cells. 5, ascospore of *Sporormia fimetaria*, multiseptate. 6, chain of conidia of *Cystopus candidus*, showing the narrow necks connecting the conidia, which dissolve in water at maturity, liberating the conidia as a powdery mass. 7, very young progametes of *Sporodinia aspergillus*. 8, the same in an older stage; the progametes have come in contact with each other, and a portion containing the protoplasm and nucleus has been cut off from each of the gametes, these two gametes eventually forming the zygospore. 9, mature zygospore of same, the empty progametes, now termed suspensors, finally decay, liberating the zygospore. 10, chlamydospores of *Chlamydomucor*, formed interstitially in the length of a hypha. 11, zoospores of *Phytophthora infestans*. 12, oosphere of *Diplanes saprolegnoides*, showing perforations in the wall, and containing seven oospores, antheridium attached to wall on the right (after Leitgeb). 13, spore of *Botrytis* germinating and forming a chain of oidia. 14, spore of *Tilletia tritici*. All highly mag.

each other, cutting the spore up into quadrate or oblong cells; this arrangement is described as muriform. Oospores, the result of a sexual act, are always one-celled. The female organ in the young condition is called an oogonium; immediately preceding the act of fertilisation the greater portion of the protoplasm contained in the oogonium separates from the wall and forms one or several spheres, each containing one or more nuclei; these spheres are termed oospheres or eggs; after fertilisation the oospheres become surrounded by a thick cell-wall, and are called oospores.

Spores vary in form from perfectly spherical or globose, the rarest condition, through elliptical, by far the most general form, to lanceolate and acicular or needle-shaped. Some are stellate, others spirally coiled, etc.

Spores are borne singly on the sporophores, but in conidial forms it is by no means unusual for the conidia to be produced in long necklace-like chains, when they are said to be concatenate; the conidia forming such chains become free from each other at maturity.

The hymenium of a typical species of *Agaricus* presents the following different structures:—

(1) Basidia, or spore-bearing cells. Each basidium consists of a single relatively large cell, usually more or less clavate in form, and projecting from its free thickened apex are four slender, spine-like bodies or sterigmata. Each sterigma bears a single spore at its tip. Although four sterigmata is the number most frequently present, in some species the basidia bear only two sterigmata each.

(2) Paraphyses, or sterile clavate cells, usually thinner and shorter than the basidia, and more numerous. These, with the basidia, are the only constant elements of the

hymenium, the surface of which consists of their closely packed free ends, and a section through the hymenium shows the elongated cells of basidia and paraphyses closely packed side by side like the palisade cells of a leaf. The functions of paraphyses are not known. In the Basidiomycetes they originate from the same hyphae that produce basidia.

(3) Cystidia, or single cells, usually larger than basidia, and often projecting much beyond the level of the hymenium. Cystidia are present in some species and absent in others. As a rule they are more general in the older or primitive types of the Agaricaceae, as in *Coprinus* and other dark-spored genera, than in the modern white-spored types, as *Tricholoma*, *Amanita*, etc. Cystidia are more general, and undergo greater modifications of form in the older families of the Basidiomycetes, as the Thelephoraceae and Polyporaceae, than in the Agaricaceae. Regarding the functions of cystidia but little is definitely known. It has been suggested that they prevent the removal of the spores from the hymenium by slugs, snails, etc. In the genus *Coprinus*, where the cystidia are very large and conspicuous, they were considered at one time to represent male sexual organs. De Bary states that in *Lactarius deliciosus* and allied species the cystidia are filled with densely granular contents, and resemble the laticiferous tubes, and in thick sections look as though they were branches of these tubes, but closer observation showed that they sprang as branches from non-laticiferous hyphae. This statement, however, is not correct. I have described and figured cystidia in *Lactarius* and *Russula* as terminating laticiferous hyphae. Biffen has also described cystidia as terminations of the conducting system in *Collybia velutipes*, where they can be

distinguished from other cells of the hymenial layer at an early period of development, when the sporophore is only three mm. high.

In the Protobasidiomycetes the basidia are septate, and hence composed of more than one cell. In the Auricularieae the basidia are cylindrical and transversely septate, each cell producing one sterigma. In the Tremellaceae the subglobose basidium is divided into four cells by two

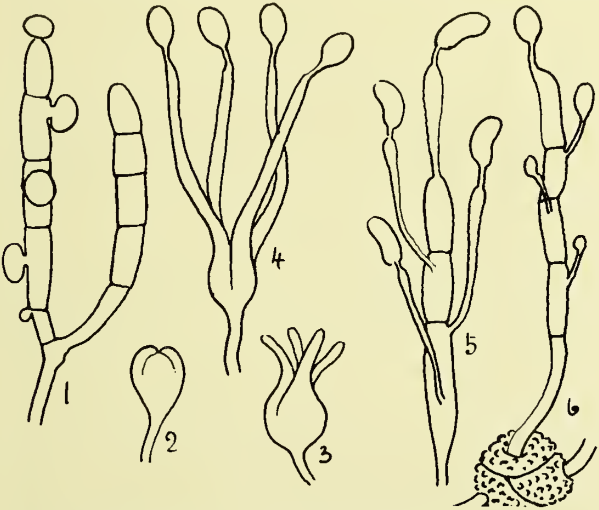

FIG. 16.—Typical basidia of Hemibasidiomycetes. 1, basidium of *Pilacre Petersii*; compare with fig. of basidium of *Tulostoma mammosum*; 2-4, basidia of *Tremella lutescens*, at different ages; 5, basidium of *Exidia auricula-judae*; 6, germinating spore of *Triphragmium ulmariae*; the promycelium or first product of germination is limited in growth and is divided into three or four cells: each cell bears a secondary spore. All highly mag.

vertical septa formed at right angles. Each of the four cells grows upwards into a long, stout sterigma.

In the Ascomycetes the ascus or spore mother-cell varies much in size and form in different groups. It is usually comparatively large, and varies from almost globose or broadly piriform in the Erysipheae, to narrowly cylindrical and elongated in many of the Discomycetes. Where the sporophore is more or less cup-shaped, with an exposed flat hymenium, as in species of *Peziza*, the asci are packed side by side like basidia, and are intermixed with slender paraphyses, and the often brilliantly coloured disc or hymenium is due to coloured pigment present in the swollen tips of the paraphyses.

The hyphae bearing the asci—ascogenous hyphae—originate from the oogonium or female sexual organ after fertilisation, whereas the paraphyses are a continuation of the vegetative hyphae.

The protective portion or fruit enclosing the asci is also of vegetative origin, and usually originates as outgrowths from one or more cells situated immediately below the oogonium. The fruit varies much in form and texture. In many of the Sphaeriaceae it takes the form of a sphere, or is more frequently flask-shaped, with a more or less pronounced neck through which the spores escape when mature. A structure of this kind is called a perithecium. The perithecium may have no external opening, and consequently has to decay or rupture irregularly before the spores are liberated, as in the Perisporieae; or it is furnished with a definitely formed opening or ostiolum, through which the spores escape as in Sphaeriaceae.

When the hymenium is enclosed in a perithecium or other structure, as in *Eurotium*, *Sphaeria*, and the puff-balls, *Lycoperdon*, etc., the fruit is said to be angiocarpous, whereas when the hymenium is exposed, as in *Agaricus*, *Polyporus*, *Clavaria*, *Peziza*, etc., the fruit is described as gymnocarpous.

Biffen, *Journ. Linn. Soc.*, 34, p. 147 (1898).

De Bary, *Fungi*, *Mycetozoa, and Bacteria* (Engl. ed.), pp. 54, 304.

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Brefeld, *Unters. Mykol.*, numerous examples of morphological details in every volume.

FORMATION OF SPORES

(*Axygospores*, *Chlamydospores*, *Conidia*, *and Zoospores.*)

In the nearly fully developed ascus of a typical ascomycetous fungus, the basal portion of the ascus contains frothy, much-vacuolated protoplasm ; in the upper portion of the ascus the protoplasm is dense and minutely granular. At this stage only one nucleus is present, situated in the dense protoplasm, which by division forms two daughter-nuclei. These, by repeated division, give origin to eight nuclei. Nuclear division is karyokinetic. According to Harper the spores are formed by an area of protoplasm being cut out of the general mass of protoplasm by the

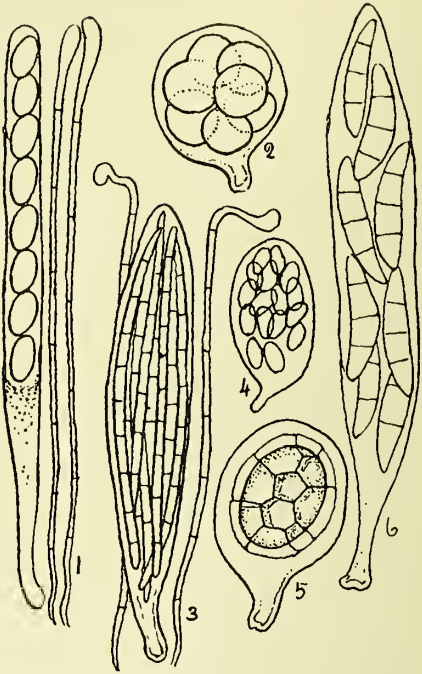

FIG. 17.—Typical forms of asci. 1, ascus containing eight spores in uniseriate order, and accompanied by two paraphyses, of *Peziza cerea*; 2, *Sphaerosoma Leveillei*; 3, *Geoglossum Peckianum*, eight long multiseptate spores arranged in a fascicle : the paraphyses are curved at the tip; 4, *Ryparobius sexdecemsporus*, ascus containing sixteen spores; 5, *Tuber excavatum*, ascus containing one large spore : some asci contain two somewhat smaller spores; 6, *Zignoella corticola*, containing eight triseptate spores, irregularly biseriate in arrangement.

activity of the fibrillae of an aster attached to each nucleus. These fibrillae rotate and bend down around the nucleus from the centre of the aster, and delimit a certain amount of protoplasm which, after becoming rounded off and bounded by a wall, constitutes a spore. After the formation of the spores is completed, a certain amount of unused protoplasm, now termed epiplasm, remains in the ascus, which, being without nuclei, undergoes disintegration. Spores produced in asci are often called ascospores. Harper suggests that the term 'free cell formation' should be confined to cells formed as described above. The two characteristic features of the process are, the cutting out of the mass of protoplasm that forms the spore by the activity of the fibrillae of an aster, and the presence in the ascus of an amount of epiplasm, or surplus protoplasm, after the spores are formed. This method of spore-formation has been observed in widely separated members of the Ascomycetes; it is not, however, universal. Guilliermond states that in *Peziza rutilans*, where the nuclei are exceptionally large, the nuclear membrane disappears during division, and there is no evidence of the existence of either centrosomes or asters. In *Taphrina Johansoni*, according to Ikeno, the process of spore-formation in the ascus does not conform with the method described by Harper, neither is it due to cleavage lines as in the Phycomycetes. Two nuclei present in the young ascus fuse and form a nucleus with a very conspicuous nucleolus. The nuclear membrane disappears, and the nucleolus, which appears to be chromatic in nature, undergoes fragmentation without any sign of mitotic division. The chromatin fragments collect in groups in vacuoles, and each group attracts a certain amount of protoplasm, which becomes surrounded by a wall and forms a spore. In *Eremascus* and *Dipodascus* there is no trace of epiplasm in the ascus.

The oospore is formed as follows: The oosphere is differentiated owing to a concentration of protoplasm in the central portion of the oogonium. The primitive wall of the oospore is formed immediately after fertilisation; afterwards the epispore is formed from the periplasm, or portion of protoplasm in the oogonium left outside the oospore. In some instances the wall of the oogonium also remains, and forms an additional protective covering to the oospore. The wall of the mature oospore is thick, and usually stratified.

Zygospores are formed by the union of two gametes; when these meet, each gamete replete with cytoplasm is cut off from its supporting hypha by a cross-wall; the double wall, where the two gametes join each other, is absorbed, and the contents of the gametes mingle to form a zygospore. When the union of the gametes is complete, thickening and cuticularisation of the epispore commences from a circular zone corresponding to the original line of union of the two gametes.

In the Saccharomycetes, or Yeasts, three modes of spore-formation are known. 1. By budding, a purely vegetative form of reproduction. When conditions of growth are favourable, a yeast-cell, which constitutes an individual, puts out a bud or swelling from any part of its surface. This bud continues to increase in size, being attached to its parent cell by a narrow neck across which a septum is formed, and finally becomes free. When growth is very vigorous, a cell may produce two or more buds or daughter-cells from different parts of its surface. These daughter-cells may in turn produce other buds, so that short chains of cells representing different generations may appear before the first daughter-cells become free from the original mother-cell. Finally all the cells become full-grown and free, and in turn constitute the mother-cells of future generations. It is mostly by means of this rapid asexual mode of reproduction that yeast is formed in such enormous quantities in breweries. 2. The formation of so-called endospores, from two to four in number, within a mother-cell. There is no evidence of any sexual act. Endospores are obtained by placing well-nourished young yeast-cells on moist slices of potato, carrot, etc., well supplied with air. After a few days the protoplasm of the cells undergoes concentration into two to four masses, each of which becomes surrounded by a cell-wall. When mature, the spores become free by the rupture of the mother-cell. In the *Zygosac-*

FIG. 18.—1, *Saccharomyces cerevisiae*; *a*, reproduction by budding or gemmation; *b*, cells containing ascospores. 2, *Zygosaccharomyces Barkeri*, showing stages in the conjugation of two cells; in the right-hand fig. four ascospores are present. (Fig. 1 after Hansen, fig. 2 after Barker.) All highly mag.

charomycetes the formation of endospores or, properly, ascospores, is the result of a sexual act. 3. In some species ordinary cells become thick-walled and form resting-spores.

In the Basidiomycetes the spores are formed by what De Bary terms acrogenous abjunction. The mother-cell, or basidium, is surmounted by a definite number of slender outgrowths—most frequently four—called sterigmata. The apex of each sterigma becomes swollen and forms a spore which at length is cut off from its sterigma by a cross-wall or septum. Spores formed on basidia are often called basidiospores. In the Hymenomycetes the spores separate from the apex of the sterigma, leaving the latter attached to the basidium. In the genera *Lycoperdon* and *Bovista*, belonging to the Gasteromycetes, the sterigma remains attached to the spore when it is shed, hence the spore with its attached sterigma resembles a miniature drum-stick. In the genus *Calocera* and *Dacryomyces* each basidium bears only two sterigmata, whereas in *Octaviania*, *Hymenogaster*, and others of the subterranean forms, the number of sterigmata is variable. Finally, in some of the Gasteromycetes sterigmata are absent, and the spores spring direct in a sessile manner from the apex of the basidium. This occurs in species of *Geaster*, *Polysaccum*, *Phallus*, *Scleroderma*, etc. No basidium produces more than one crop of spores, and these are developed simultaneously.

It has been known for some time that the formation of spores contained in sporangia in the members of the Mucorineae presented some peculiarities. Léger investigated this subject, and showed that in all cases a differentiation of the protoplasm contained in the sporangium into a dense peripheral portion and a less dense central portion occurred; that numerous nuclei were present, and that

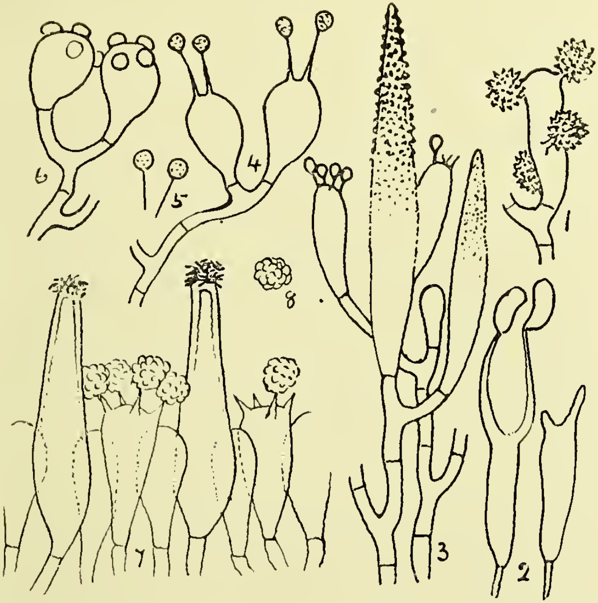

FIG. 19.—Typical forms of basidia in the Basidiomycetes. 1, basidia and spores of *Tulostoma mammosum*: the basidia are elongated, and the spores grow along its length as in the Hemibasidiomycetes, but the basidium is not septate. 2, bisporous basidium of *Dacryomyces deliquescens.* 3, basidia and fusiform cystidia having the upper portion covered with particles of oxalate of lime, of *Peniophora inconspicua.* 4, bisporous basidia of *Lycoperdon echinatum.* 5, two spores of same showing the persistent sterigmata. 6, tetrasporous basidia with sessile spores, of *Scleroderma vulgare.* 7, portion of hymenium of a typical agaric, *Inocybe asterospora*, showing tetrasporous basidia; paraphyses, somewhat smaller than the basidia, and not bearing sterigmata; cystidia, longer than the basidia. In many species of *Inocybe*, like the present one, the cystidia, when mature, are crowned by an amorphous mass, resembling a cluster of dark-coloured crystals. This is caused by the exudation and hardening of the contents of the cystidium. 8, free spore of No. 7. All highly mag.

finally the denser portion was cut up into polygonal portions, each of which a became a spore.

Swingle has recently added very materially to our knowledge as to the exact mode of spore-formation in *Rhizopus nigricans* and *Phycomyces nitens.* At first there is no columella present in the sporangium, into which there is a streaming of cytoplasm, nuclei, and vacuoles, forming a dense layer containing many nuclei near the periphery, and a less dense central portion containing fewer nuclei. Next there is formed a layer of comparatively large, round vacuoles near the inner zone of the denser protoplasm. These vacuoles become flattened and fuse together, forming a circular cleft in the dense protoplasm, thus delimitating the columella. The dense protoplasm with its numerous nuclei, situated between the columella and the sporangium wall, is broken up; in *Rhizopus* by furrows advancing inwards from the sporangium wall, and outwards from the columella cleft, both systems branching, curving, and cutting out numerous multinucleate portions of protoplasm, which, after becoming rounded off and provided with a cell-wall, constitute the spores, separated by the secretion of an intersporal slime. Simultaneously the columella forms a wall, and its contained nuclei undergo partial disintegration.

In *Phycomyces* the spore-plasma is cut up into multinucleate portions homologous to those in *Rhizopus*, by angles forming in certain vacuoles, which extend as branching clefts, meeting others of a similar nature starting from the columella. The furrows are partly filled with the contents of the vacuoles that formed the cleavage lines.

During the process of spore-formation the nuclei remain in a resting condition.

The mechanics of this method of division are at present unknown. Swingle suggests local contractions of the cytoplasm. Harper uses the term 'cleavage by constriction' for this process, and points out that it should be very carefully distinguished from free cell formation, inasmuch as there can be no epiplasm; hence the process is initiated from the plasma membrane situated either on the periphery of the sporangium, or surrounding the vacuoles, and not from any stimulus of nuclei, or fibrillae, or an aster.

As previously stated, Brefeld's view as to the homology between sporangia and asci, or the derivation of the latter from the former, is not supported by recent cytological research, inasmuch as it is difficult to conceive such diverse characters manifested by the protoplasm of homologous organs; there are, however, transitional modes of spore-formation in both groups.

In the majority of the Mucorineae the sporangia are spherical or hemispherical, but in the section called Syncephalideae the sporangia present a quite different appearance. At the apex of an elongated sporangiophore is a swollen head from which spring numerous closely packed, narrowly cylindrical bodies, each usually containing a single row of superposed spores, the whole resembling an *Aspergillus* head. The origin of these spores has been variously interpreted. De Bary and Woronin, Brefeld and Fischer consider them as exogenously formed conidia, the latter urging the absence of transitional forms between cylindrical and the typical spherical sporangia as precluding their being sporangia. Léger, however, has shown that these cylindrical bodies are true sporangia, filled with protoplasm containing numerous nuclei, which becomes cut up simultaneously into spores separated by hyaline portions of protoplasm. Thaxter has corroborated Léger's statement, and in addition has described a species of *Syncephalastrum* in which the sporangia are more or less clavate or swollen at the apex, and having more than a single row of spores in the swollen portion, thus forming a connecting link between globose and cylindrical sporangia.

Not unfrequently in certain members of the Mucorineae, *Absidia*, and certain species of *Mucor*, the gametes do not come in contact, yet each branch forms a body similar in appearance to a zygospore, and equally capable of germination; in other instances similar bodies are produced singly and not in pairs; such structures are called azygospores. Whether these bodies, apart from fecundation, agree cytologically with normal zoospores, is not known.

Chlamydospores are usually distinguished among asexual spores by not being borne on specialised sporophores, but occur in chains in the length of ordinary vegetative hyphae. Alternate cells of the chain become enlarged by absorbing the protoplasm of adjoining cells, and assume a barrel-shape with a thick cell-wall. These, when mature, are liberated by the dissolution of the alternate empty cells. Brefeld has dealt in detail with chlamydospores in *Chlamydomucor racemosus*, *Nyctalis*, and *Oligoporus*. Ward has also noted their presence in *Onygena equina*. In some instances chlamydospores are formed on very short lateral branches springing from prostrate hyphae, as in *Mycogone*, a conidial form of *Hypomyces*. Respecting the mode of origin of zoospores, which are produced by some species belonging to the Phycomycetes, our knowledge is incomplete. Wager states that from five to eight nuclei are present in the zoosporangia of *Cystopus candidus* when cut off from the sporangiophore by a septum. Each nucleus remains undivided and forms the nucleus of a zoospore. The zoospores are formed, according to Büsgen, by simultaneous division of the protoplasm contained in the zoosporangium into several distinct portions. According to Rothert, the zoospores of *Saprolegnia* are diplanetic, or have two distinct periods of movement. During the first period they have two cilia of equal length inserted at the summit. After a short period of activity the spore becomes clothed with a thin membrane. The zoospore then emerges through a narrow slit in this membrane, furnished with two cilia of unequal length, and inserted laterally. After a second short period of motility, the zoospore comes to rest, forms a new membrane, and is at once capable of germination. The zoospores of the Peronosporeae, including *Pythium*, are monoplanetic, or have only one period of motility, which corresponds to the second stage of those of the Saprolegniaceae. After the first period of motility of the zoospores in the Saprolegniaceae the cilia are withdrawn into the zoospore. In the second condition in *Saprolegnia*, and at the end of the only motile phase in the Peronosporeae, the cilia are not absorbed by the zoospore, but remain outside and disappear.

In *Myrioblepharis paradoxa* Thaxter states that the zoospores are thickly covered all over with cilia. This structure is unique in the fungi, and elsewhere only occurs in *Vaucheria*, an alga.

Conidia generally may be distinguished from chlamydospores by having a thin cell-wall, and by being terminal on more or less specialised branches called conidiophores. The majority of conidia are formed by acrogenous abjunction, or the delimitation of an apical portion of the hypha, which becomes a conidium. Conidia may be produced

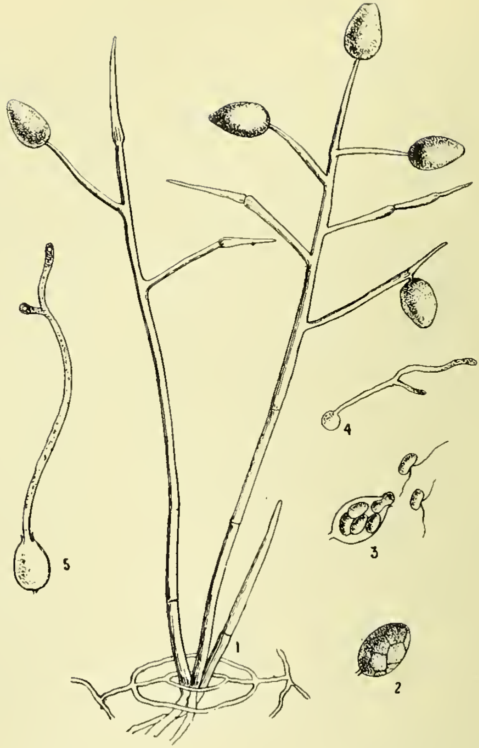

FIG. 20.—*Phytophthora infestans*, a fungus whose asexual reproductive bodies are usually motile zoospores. The sexual mode of reproduction has disappeared. In allied species the conidia do not contain zoospores, but produce a germ-tube on germination. This sometimes happens with *P. infestans*, which thus illustrates a fungus occupying a transitional stage between the older aquatic types which constantly produce zoospores, and the more modern types, where the conidia are dispersed by wind, and on germination produce a germ-tube or hypha, which enters the host. 1, a cluster of branched conidiophores emerging into the air through the stoma of a potato leaf; 2, a free conidium showing its contents breaking up into zoospores; 3, a conidium liberating its zoospores; 4, a zoospore that has become passive and is germinating by emitting a germ-tube; 5, a conidium germinating by the protrusion of a germ-tube. All figs. mag.

singly, as in *Peronospora*, *Botrytis*, etc., in clusters, capitate, from the swollen apex of a hypha, as in *Cephalosporium*;

FIG. 21.—*Cercospora circumscissa*, a fungus whose conidial fruit consists of a single conidium produced at the tip of a short, unbranched conidiophore. 1, peach leaf showing blackened spots caused by the fungus. The small circular patches of leaf tissue killed by the fungus soon dry up and fall, leaving a number of holes in the leaf, hence the popular name of 'shot-hole fungus.' 2, a cluster of conidiophores bearing septate conidia. Fig. 1, nat. size; fig. 2, mag.

or in chains, concatenate, as *Penicillium*, *Cystopus*, *Aegerita*, etc. When conidia are produced in chains the order of development may be basipetal, the youngest conidium being situated at the base of the chain, as in *Penicillium*, *Cystopus*, etc.; or the order of development may be acropetal, the youngest conidium being situated at the apex of the chain, as in *Heterosporium*, *Cladosporium*, etc.

FIG. 22.—*Melampsora pinitorqua*, a fungus whose aecidiospores are produced in chains. 1, top of a young pine attacked by the aecidial form of the fungus; 2, three chains of aecidiospores in different stages of development; 3, an aspen leaf with pustules formed by the teleutospore stage of the fungus; 4, section through a pustule or sorus of teleutospores, as yet covered by the epidermis of the leaf. Figs. 1 and 3, rather less than nat. size; the remainder mag.

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SEXUAL REPRODUCTION

Recent research has demonstrated the existence of what appear, at first sight, very different modes of sexual reproduction in fungi, and although these diverse modes are being to some extent linked up by the discovery of intermediate conditions, yet our knowledge is too limited in this direction to serve as the basis of a phylogenetic classification.

If we accept Brefeld's idea as to the evolution of the fungi, commencing with the algae-like Phycomycetes, from which descended the Ascomycetes, and finally the Basidiomycetes, there is an evident reduction of the sexual mode

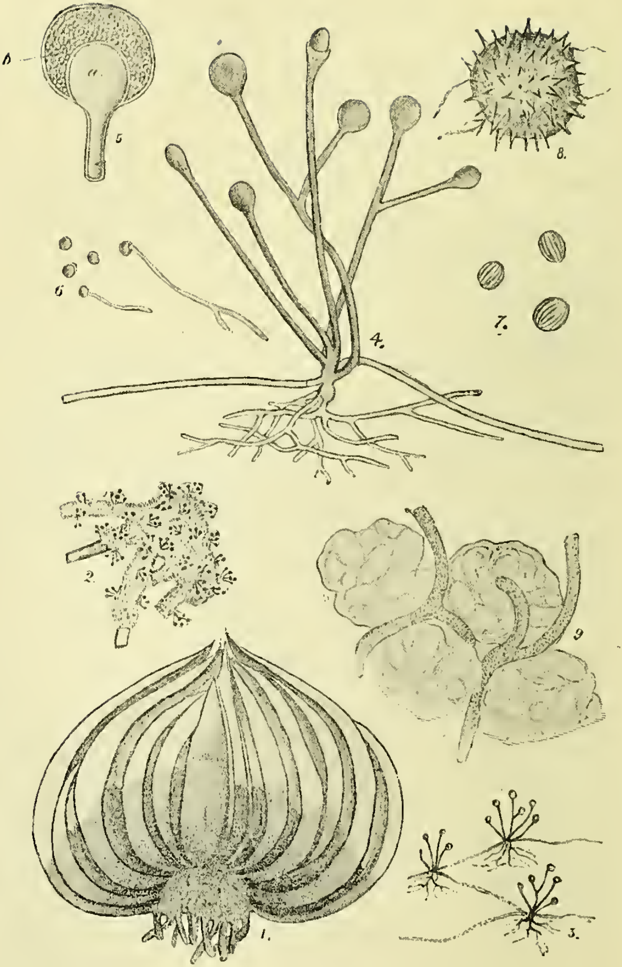

FIG. 23.—*Rhizopus necans*, a fungus whose sexual product is a zygospore. 1, section of a lily bulb attacked by the fungus, the dark portion is infected by the parasite; 2 the fungus bearing conidial fruit and showing the habit

[*Description continued on p.* 67.

of reproduction following the sequence of differentiation; commencing in the earliest group, the Phycomycetes, continued to a greater extent in the Ascomycetes, and entirely absent from the most modern group, the Basidiomycetes.

From the present standpoint of knowledge Brefeld's scheme of evolution of the fungi is not generally accepted for the following reasons. In the Saprolegnieae, Peronosporaceae, and some other groups belonging to the Phycomycetes, the sexual organs consist of an antheridium and an oogonium, which are homologous with the sexual organs of *Vaucheria*, an alga considered by some as representing the group of algae from which the fungi descended.

In the Mucorineae, another group included in the Phycomycetes, the sexual organs consist of two specialised portions of hyphae called gametes. By the union and fusion of the contents of two progametes a zygospore is formed. Perhaps these gametes are but modifications of the antheridium and oogonium of the older groups, Peronosporeae, etc. In some species the two gametes differ in size and other respects; in others the two gametes are at all events morphologically similar.

In some Ascomycetes antheridia and oogonia are still present, and of functional value, in widely separated groups. There is also present in the Ascomycetes a second type of sexual reproduction, in which the receptive cell, the equiva-

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of growth; 3, conidial fruit on a larger scale; 4, a single cluster of conidial fruit or sporangia, showing the rhizoids or vegetative hyphae at the base; 5, optical section of a sporangium: *a*, columella: *b*, sporangial sac filled with spores (technically conidia); 6, spores from sporangium, some germinating; 7, spores on a larger scale to show markings on epispore; 8, mature zygospore, the suspensors are indicated; 9, mycelium running between cells of bulb containing starch. Figs. 1 and 2, nat. size; rest mag.

lent of the oogonium, is surmounted by a more or less elongated filament called a trichogyne. The fertilising bodies, which consist of minute non-motile cells, adhere to the trichogyne, and after absorption pass down to the receptive cell. This second type of the sexual process is present and of functional value in the Laboulbeniaceae, and also in the discomycetous fungal element in many Lichens. In an abortive or degenerate form, evidence of this mode of sexual reproduction exists in many genera belonging to the Ascomycetes; vestiges of a trichogyne have also been shown to exist in the Uredineae. Now there is no reason for supposing other than that these two modes of sexual reproduction as presented by the fungi are totally independent in origin, and furthermore, as an exactly similar mode of reproduction with trichogyne and receptive cell is characteristic of the Florideae or red seaweeds, it is suspected that different groups of fungi have originated independently from the algae, and that the phylogenetic affinity between such groups of fungi and the algae from which they evolved is indicated by homology of the sexual organs in fungus and alga respectively.

As previously stated, the most important point in connection with sexual reproduction consists in the fusion of two nuclei, male and female respectively. A certain amount of cytoplasm passes along with the male nucleus into the female receptive cell, but the significance of this act is considered as of secondary importance as compared with the fusion of sexual nuclei. The discovery of the fusion of numerous male and female nuclei in pairs in the oosphere of *Cystopus bliti* was considered at the time by some as of primary importance, and the coenocyte went up several degrees in the estimation of those who saw in this discovery evidence of a distinct coenogynetic phylum. The next instalment of discovery announces that in one and the same genus, *Cystopus*, fertilisation may be represented by the fusion of numerous male and female nuclei in pairs; by the fusion of comparatively few pairs, or finally by the fusion of a single male and female nucleus, as in *Cystopus candidus*. In *Pyronema confluens*, one of the Discomycetes, numerous male and female nuclei fuse in pairs. Woronin has shown that in the conidial condition of *Sclerotinia fructigenum*, the conidia and vegetative hyphae are multinucleate. *Sclerotinia* also belongs to the Discomycetes, and it would be interesting to know whether the multinucleate character is constant throughout the Discomycetes.

If we include as a trichogyne the elongated body springing from the apex of the oosphere in *Pyronema*, then the male nuclei, along with a certain amount of cytoplasm, pass into the trichogyne from an antheridium which fuses with the trichogyne. In *Collema* the male bodies or 'spermatia' are produced in special receptacles or spermogonia, as is the case in the aecidia of the Uredines. In the Laboulbeniaceae the male bodies are in some species endogenous, or produced in special receptacles; in others exogenous, and borne singly at the tips of special branchlets. In all, the male fertilising body is non-motile.

The apparent striking difference between the various modes of fertilisation indicated in the foregoing pages will, in all probability, disappear as our knowledge increases; what are now considered as types of different methods may prove to be no more than modifications of one or a few fundamental types. It must be remembered that at the present moment we are not acquainted with the mode of fertilisation, from a modern cytological standpoint, of more than about twenty species, and even among these, the crucial evidence, the fusion of nuclei, is in some instances only assumed; hence critical discussion and philosophical speculation are equally unsafe.

Wager points out that three methods of fertilisation occur in the Peronosporeae alone. (1) Uninucleate oosphere, binuclear fusion, and uninucleate oospore (*P. parasitica*). (2) Uninucleate oosphere, binucleate fusion, and multinucleate oospore (*C. candidus*, *C. portulacae*, and *P. ficariae*). (3) Multinucleate oosphere, multinuclear fusion in pairs, and multinucleate oospore (*C. bliti*).

Fisch states that in *Pythium* the nuclei of the oogonium fuse together to form one female nucleus, and that the one nucleus in the antheridium is also probably the result of fusion of several nuclei. In the process of fertilisation the male nucleus enters the oogonium and fuses with the female nucleus to form the first nucleus of the oospore. If this account is corroborated, it will constitute a fourth type.

The difference of opinion respecting the occurrence of fertilisation in the Saprolegniaceae has at last been set at rest by the investigations of Trow, who has demonstrated an undoubted sexual process in several members of the family. The following is an abridged account of his researches on *Achlya debaryana* of Humphrey (=*Achlya polyandra*, De Bary). The antheridia and oogonia are multinucleate; the nuclei in both organs divide indirectly, and there are apparently eight chromosomes at this stage. Some of the nuclei in both organs undergo a second division in which the number of chromosomes is apparently reduced to four. The number of nuclei in the

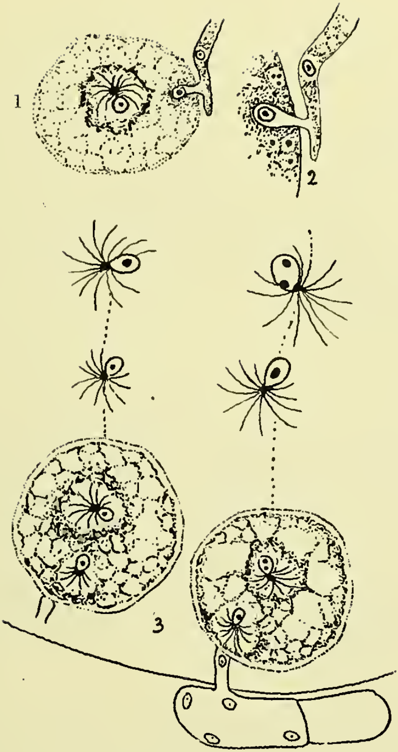

FIG. 24.—1, median section of a young oospore of *Achlya debaryana*, showing female nucleus, centrosome, and astrosphere, the entry of the sperm nucleus and the presence of the receptive spot; 2, portion of fig. 1 more highly mag.; 3, young oospores of *A. debaryana* in which the wall is clearly visible. The mode of attachment of the fertilisation tubes is illustrated. The rays of the male astrospheres are directed outwards. (After Trow.) All highly mag.

oogonium become reduced, due to disintegration, and at the period of 'balling,' or the breaking up of the protoplasm present in the oogonium into a number of spheres—oospheres, each oosphere contains only one nucleus. The single nucleus of the oosphere is associated with a well-developed centrosome and astrosphere; there is also present a coenocentrum, or ovocentrum, as it is termed by Trow. After the formation of oospheres, fertilisation tubes from the antheridia grow into the cavity of the oogonium, and when they reach the oospheres, these acquire a cell-wall and a second nucleus. The antheridial tubes often produce a lateral branch in the oogonium, which comes in contact with and fertilises a second oosphere. The male nucleus after its entry into the oosphere acquires a distinct centrosome and astrosphere. When the male nucleus reaches the central region of the oospore, the dense protoplasm accompanying it goes to swell the centrally situated ovocentrum, which now encloses two nuclei, two centrosomes, and two astrospheres. The fusion of the male and female nuclei does not take place until centrosomes, astrospheres, and coenocentrum have disappeared.

Fertilisation takes place in *Peronospora parasitica* as follows, according to Wager. Both oogonium and antheridium are multinucleate. Previous to fertilisation the protoplasm in the oogonium becomes differentiated into a distinctly marked peripheral, granular, homogeneous portion termed periplasm, and a vacuolate central portion, the ooplasm. This period has been termed the stage of zonation. All the nuclei pass into the periplasm and undergo mitosis. The nuclei in the antheridium also undergo division, and this organ becomes closely attached

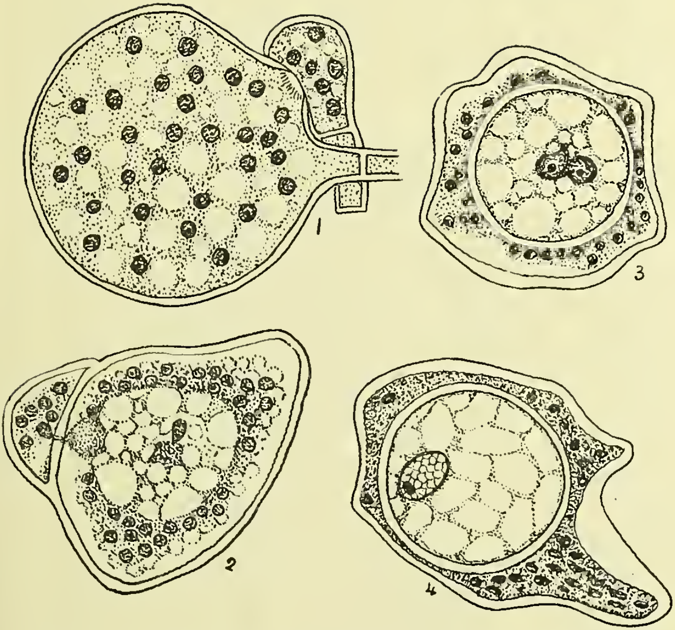

FIG. 25.—Different stages in the fertilisation of *Peronospora parasitica.* 1, young oogonium with antheridium and receptive papilla, where the antheridium is in contact with the oogonium; numerous nuclei are present in each organ. 2, the central body (coenocentrum) is very distinct, and a single nucleus from the periplasm is in contact with it. A nucleus is just about to pass from the antheridium into the fertilising tube. 3, showing the sexual nuclei in contact and just beginning to fuse. The wall of the oospore is now formed separating the ooplasm from the periplasm. All the nuclei originally in the oospore, with the exception of the one female nucleus that is fusing with the male nucleus, now lie in the periplasm. 4, the fusion nucleus, resulting from the fusion of the male and female nuclei, shows a distinct network and a single nucleolus. (After Wager.) All highly mag.

to the wall of the oogonium. At the point of contact the wall separating the oogonium from the antheridium becomes very thin, and a slight hyaline protoplasmic papilla is formed, which slightly projects into the antheridium. This structure, called the receptive papilla, seems to be in some way connected with the perforation of the oogonial wall and the formation of the fertilising tube. After the differentiation of the ooplasm, a denser mass termed a coencentrum appears in its centre, and one of the nuclei formed by division in the oogonium comes into close contact and is eventually embedded in it. The fertilising tube of the antheridium enters the oogonium at the point where the receptive papilla is formed, and increases in length until it reaches the coenocentrum with its embedded female nucleus. At this stage the apex of the antheridial tube opens, and the male nucleus escapes and comes into contact with the coenocentrum. The male and female nuclei do not fuse at once, but remain apart until the oospore is nearly ripe, when fusion takes place, consequently the mature oospore is uninucleate. *Peronospora parasitica* is the only known member of the Peronosporeae having retarded nuclear fusion in the oospore. This feature is, however, not uncommon, and may occur in *Spirogyra*, *Cosmarium*, and *Basidiobolus*. In some instances fusion is retarded until germination commences, as in *Polyphagus*.

In *Cystopus candidus*, another member of the Peronosporeae, fertilisation, as described by Wager, conforms in essential features with that recorded for *Peronospora*. The oogonia and antheridia are both multinucleate, and the nuclei undergo karyokinetic division. After the zonation period in the oogonium and the formation of a coenocentrum in the ooplasm, a single nucleus becomes embedded in the coenocentrum. A receptive papilla is formed at the point where the antheridium is applied to the wall of the oogonium. An antheridial tube enters

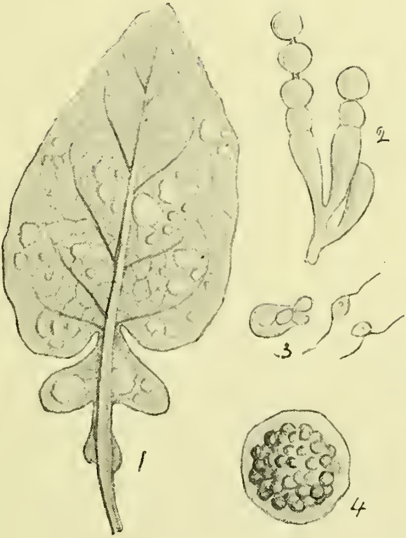

FIG. 26.—*Cystopus candidus*. 1, the fungus forming white patches on a cabbage leaf; 2, chains of conidia in different stages of development; 3, conidium germinating and liberating zoospores; 4, ripe oospore. Fig. 1, reduced; the others mag.

the oogonium and liberates a nucleus, which comes in contact with the coenocentrum and its contained female nucleus. The two nuclei remain in contact for a short time and then fuse together to form the first nucleus of the oosphere. At this stage the formation of a wall round the oospore commences, separating it from the peripheral periplasm. From this stage of development the conditions differ from those present in *Peronospora*. The single nucleus divides into two, each daughter-nucleus again divides, making four nuclei in the oospore. The four nuclei then divide into eight, and successive division continues until there are thirty-two nuclei present. By the time this number of nuclei are produced, the exospore and endospore are fully formed and the oospore is mature. The oospore now enters on a resting-stage after having germinated to the extent of what may be regarded as a multinucleate cell or sporophyte containing thirty-two nuclei.

Wager did not have an opportunity of observing the germination of the oospore, but points out that De Bary states that in germination the oospore becomes a zoosporangium, liberating one hundred or more zoospores. From this it is considered probable that if at a later period each of the thirty-two nuclei divided into four, one hundred and twenty-eight nuclei would be present, which would be sufficiently near De Bary's number of zoospores, allowing one nucleus for each. Hence Wager considers that we may regard each of the thirty-two nuclei, together with the protoplasm in connection, as the mother-cell of four zoospores, and the mature oospore with the thirty-two nuclei as the sporophyte. The life-history of *Cystopus candidus* might then be represented by the following diagram :—

Gametophyte.—The vegetative hyphae bearing zoosporangia and sexual organs.

Oogonium. **Antheridium.**

Oosphere, with ovum nucleus. Fertilising tube with male nucleus.

Oospore.—Uninucleate.

Sporophyte.—Resting oospore, multinucleate.

Sporangium.—Each nucleus of sporophyte divides to form the nuclei of four spores.

Zoospores.

Gametophyte.

In *Cystopus bliti*, according to Stevens, the general phenomena of fertilisation agree with those in *Cystopus candidus*, with the exception that the ooplasm of the oogonium contains numerous nuclei. The antheridial tube liberates about one hundred nuclei into the oogonium, and these fuse in pairs with the female nuclei. This results in the presence of numerous fusion nuclei in the oosphere in place of one, as in *Cystopus candidus*. Stevens calls this structure a compound oosphere. The fusion nuclei remain throughout the winter unchanged.

Other species of *Cystopus* have been examined having a smaller number of fusion nuclei in the oospore than in *Cystopus bliti*; in fact there appears to be a sequence of species of *Cystopus* ranging, so far as numbers of fusion nuclei present in the oospore is concerned, from *Cystopus bliti* with its numerous nuclei to *Cystopus candidus*, where only a single nucleus is present. Such a sequence occurring among closely allied species seems to indicate the gradual change from a primitive form, where numerous nuclei in the oospore was general, to the more usual condition met with at the present day when only one nucleus is present.

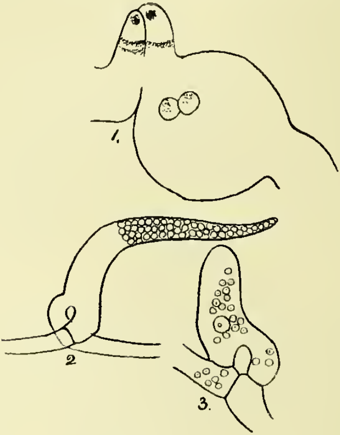

FIG. 27.—1. *Basidiobolus ranarum*, nuclei in beaks becoming disorganised: the male nucleus has passed into the enlarged female gamete, and has approached the female nucleus (after Fairchild). 2-3, *Dipodascus albidus*; 2, showing the mature ascus containing numerous spores (after Lagerheim); 3, young ascus of *Dipodascus albidus*, showing the one large nucleus which by division forms the nuclei of the spores (after Juel). All highly mag.

A somewhat primitive type of zygospore formation presented by *Basidiobolus ranarum* has been investigated in detail by Fairchild. Two contiguous cells of an ordinary vegetative filament each develop a protuberance or gamete.

These gametes grow up in contact, but are at first separated at the base by the cross-wall dividing the mother-cells of the gametes. A single nucleus from the mother-cell passes into each gamete and undergoes karyokinetic division. One of the resulting daughter-cells passes to the apex of each gamete, where it is cut off from the remaining portion of the gamete by a cross-wall. At this stage a perforation appears in the wall separating the two gametes, the female gamete increases much in size, and the male nucleus passes through the perforation in the cross-wall and comes in contact with the female nucleus. The cytoplasms of both gametes combine to form the zygospore, which first forms quite a thin wall; inside this the thick, several layered endospore is slowly formed. The male and female nuclei have fused by the time the zygospore has reached maturity.

The formation of zygospores in the Mucorineae has been studied by Léger, and the following is his view on the subject. Two gametes, often identical in size and structure, and replete with cytoplasm and numerous nuclei, approach each other; the contents of each gamete is cut off from its supporting hypha by a cross-wall, and the double wall where the two gametes touch each other is absorbed. Soon after this stage is reached the cytoplasm diminishes in volume, and eventually all the nuclei disappear. At this moment two groups of small spheres appear; these bodies, which are dense and granular, are termed embryogenic spheres. At a later stage the small spheres of each group fuse together to form a large sphere. These two spheres, which become clothed with a double membrane, are called embryonic spheres. At the moment of germination of the zygospore the two embryonic spheres lose their membrane, increase in size, and fuse together. At this stage nuclei appear in the mass formed by the two fused embryonic spheres, and undergo karyokinetic division before they pass into the germ-tube. Léger says that azygospores present exactly the same phases of development as zygospores; the only point of difference being that in azygospores only one embryonic sphere is present instead of two, as in the zygospore.

The above account leaves much to be desired respecting the behaviour of the nuclei. Grüber has examined *Sporodinia grandis* and considers the presence of Léger's embryonic spheres as doubtful. The subject of sexuality in the Mucorineae has quite recently been prosecuted from a new standpoint by Blakeslee. This author observed that some species, as *Sporodinia grandis*, could be readily induced to produce zygospores on a suitable substratum by sowing spores from a single sporangium. On the other hand, it was found that many other species, of which *Rhizopus nigricans* may be taken as a type, would never form zygospores from the product of a single sporangium, but only when a mass of spores from a zygosporic culture was used. When isolated cultures of the last-named species were grown in proximity on nutrient agar, it was observed that zygospores were formed at the junctions of the two colonies. This suggested the idea that this species consisted of two strains or races which, when grown apart, produce only sporangia, but which produce zygospores when the two physiologically different races are grown in contact. These are designated respectively × and — strains, which is considered as non-committal as to the sexual relation the strains bear to each other. This condition is essentially similar to that in dioecious plants and animals, although morphological differentiation is not so marked in the Mucorineae. The term *heterothallic* is used to designate those forms that are dioecious, as in the *Rhizopus* type; whereas *homothallic* is used for hermaphrodite forms of the *Sporodinia* type. Hybrids have been produced between + and − strains of different species of the heterothallic type. The following is the author's summary of this most interesting discovery:—

(1) The production of zygospores in the Mucorineae is conditioned primarily by the inherent nature of the individual species and only secondarily by external factors.

(2) According to their method of zygospore formation, the Mucorineae may be divided into two main groups, which have been termed respectively homothallic and heterothallic.

(3) In the homothallic group, comprising the minority of the species, zygospores are developed from branches of the same thallus or mycelium, and can be obtained from the sowing of a single spore.

(4) In the heterothallic group, comprising probably a large majority of the species, zygospores are developed from branches which necessarily belong to thalli or mycelia diverse in character, and can never be obtained from the sowing of a single spore. Every heterothallic species is therefore an aggregate of two distinct strains, through the interaction of which zygospore production is brought about.

(5) These sexual strains in an individual species show in general a more or less marked differentiation in vegetative luxuriance, and the more and less luxuriant may be appropriately designated by the use of + and − signs respectively.

(6) In heterothallic species, strains have been found which, from their failure to react with + and − strains of the same form, have been called 'neutral,' and a similar neutrality may be induced by cultivation under adverse conditions.

(7) In all species of both groups in which the process of conjugation has been carefully followed, the swollen portions (progametes) from which the gametes are cut off do not grow towards each other, as currently believed, but arise from the stimulus of contact between more or less differentiated hyphae (zygophores), and are from the outset always normally adherent.

(8) In some species the zygophores have been demonstrated to be mutually attractive (zygotactic).

(9) In the heterogamic subdivision of the homothallic group, a distinct and constant differentiation exists between the zygophoric hyphae and the gametes derived from them, but in the remaining homothallic forms and in all heterothallic forms no such differentiation is apparent.

(10) A process of imperfect hybridisation will occur between unlike strains of different heterothallic species in the same or even in different genera, or between a homothallic form and both strains of a heterothallic species.

(11) By taking advantage of this character it has been possible to group together in two opposite series the strains of all the heterothallic forms under consideration.

(12) When thus grouped the − or less luxuriant will be in one series, while the + or more luxuriant will be in the other.

(13) From the foregoing observations it may be concluded:—

(*a*) That the formation of zygospores is a sexual process;

(*b*) that the mycelium of a homothallic species is bisexual;

(*c*) while the mycelium of a heterothallic species is unisexual;

(*d*) and further, that in the + and − series of the heterothallic group are represented the two sexes.

In *Dipodascus albidus*, belonging to the Hemiasci, we have an apparently primitive mode of sexuality, admitted as such on account of the fusion of two nuclei to form a fusion-nucleus, which by repeated division produces the nuclei round which the spores are formed. From a prostrate septate, vegetative hypha, two blunt lateral outgrowths or gametes appear, separated from each other by a septum of the mother-hypha. These lateral branches or sexual cells are both multinucleate, and soon fuse together at the apex. According to Juel the nuclei in the sexual cells are indistinguishable from the vegetative nuclei, but soon after the fusion of the cells a larger nucleus appears, supposed to result from the fusion of two of the smaller nuclei. This large fusion-nucleus gives origin to a large but indefinite number of nuclei, larger than the vegetative nuclei. These large nuclei become centres of spore-formation. The apex of the fused gametes increases in length, forming an ascus-like body containing the spores. The vegetative nuclei remain with the cytoplasm at the base of the spore-sac. The number of spores contained in the spore-sac or ascus is variable in different individuals.

Fertilisation in *Sphaerotheca Castagnei*, one of the Erysipheae, belonging to the Ascomycetes, has been studied by Harper. The antheridium and oogonium originate as lateral branches from adjoining hyphae. Each at first contains a single nucleus and dense protoplasm, and at an early period of development, both are cut off from their supporting hyphae by a cross-wall. When the oogonium is fully developed, the antheridial branch, which is closely applied to the wall of the oogonium, increases in length and its nucleus divides. One of the daughter-nuclei passes to the tip of the antheridial branch, which is cut off from the lower portion by a cross-wall, and constitutes the antheridium. By increase in length of the lower portion of the antheridial branch, the antheridium comes to rest on the apex of the oogonium. At this stage of development the nucleus of the oogonium is larger than the vegetative nuclei, and that of the antheridium smaller. The walls of antheridium and oogonium are dissolved at the point of contact, and the male nucleus passes into the oogonium and fuses with the female nucleus. After this fusion or fertilisation the opening into the oogonium closes by the formation of a new wall. After fertilisation nuclear division and cell-formation commence in the oogonium, resulting in the formation of a row consisting of five or six cells. When this is completed the second cell from the apex contains two nuclei, the other cells one nucleus each. The cell containing two nuclei forms the ascus. At a later stage the two nuclei present in the ascogenous cell fuse.

This fusion of the two nuclei in the ascogenous cell is considered by Dangeard as constituting true sexual fertilisation.

It is important to note that after fertilisation a portion of the protoplasm of the oogonium does not separate from the wall and form a distinct cell round which a wall is formed, as in in the Phycomycetes. In this particular *Sphaerotheca* and other Ascomycetes agree with the Florideae.

In *Erysiphe*, a genus allied to *Sphaerotheca*, the process is more complicated. The nucleus resulting from the fusion of the male and female nuclei in the oogonium undergoes repeated division at once until five to eight nuclei are present in the oogonium, which in the meantime has increased in length and become somewhat curved. Then, as in *Sphaerotheca*, the oogonium develops into a row of cells, each of which contains a single nucleus, except the second from the apex or the penultimate cell, which contains more than one nucleus. This cell becomes the ascogonium, and gives off from all parts of its surface ascogenous hyphae. These hyphae become divided by cross-walls into two or three cells; one of these cells, always an intercalary one, contains two nuclei and grows into an ascus. Five to eight asci become fully developed. The two nuclei in the cell forming an ascus fuse and form a fusion-nucleus, which again divides to form the nuclei of the ascospores.

In *Pyronema confluens*, also one of the Ascomycetes, investigated by Harper, the sexual apparatus is exceptionally large and conspicuous. The cells of the vegetative mycelium are multinucleate, as are also the antheridia and archegonia, which originate as in *Sphaerotheca* and *Erysiphe*. A small papilla soon appears at the apex of the oogonium, which grows into a long conjugating-tube or trichogyne. The trichogyne, like the oogonium, contains many nuclei, and, when fully developed, is cut off from the oogonium by a cross-wall, but before conjugation with the antheridium takes place, this cross-wall is dissolved; the nuclei in the trichogyne also undergo disintegration. A pore is formed at the point where the trichogyne and antheridium touch, and the nuclei and some of the cytoplasm of the antheridium pass into the oogonium. Previous to the passage of the male nuclei into the oogonium, the nuclei in the latter become massed in the centre, and after the entry of the contents of the antheridium, the male and female nuclei fuse in pairs. These paired nuclei do not afterwards fuse into a single mass. After fertilisation the oogonium, or now the ascogonium, produces ascogenous hyphae, into which the fused nuclei pass. As in *Erysiphe*, the penultimate cell of each ascogenous hypha contains two nuclei which fuse. This cell then becomes an ascus. The ascocarp in *Pyronema* is a compound body, the asci originating from several fertilised oogonia produced in a cluster.

The sexual process in *Pyronema* agrees in essential points, and is homologous with that in other Ascomycetes, as *Sphaerotheca*, *Erysiphe*, *Peziza*, *Ascobolus*, etc., and also with that of some algae, as *Nemalion*, *Batrachospermum*, etc.

According to Barker, numerous nuclei are present in the antheridium and oosphere of *Monascus*.

The most perfect form of sexual reproduction where a trichogyne is present is met with in the Laboulbeniaceae, belonging to the Ascomycetes. Our knowledge of this interesting group is due to the researches of Thaxter.

The fundamental structure in these minute fungi, which rarely attain to 1 mm. in height, is simple, the receptacle often consisting primarily of two cells; the apical cell gives origin to the branches or appendages bearing the antheridia or male organs, whereas the basal cell, after repeated division, produces the procarp or carpogenic cell, surmounted by the trichogyne. The trichogyne may consist of a single cell, or a much-branched, septate body, consisting of many cells. The free tips of the trichogyne are alone receptive, and conjugate with the antherozoids

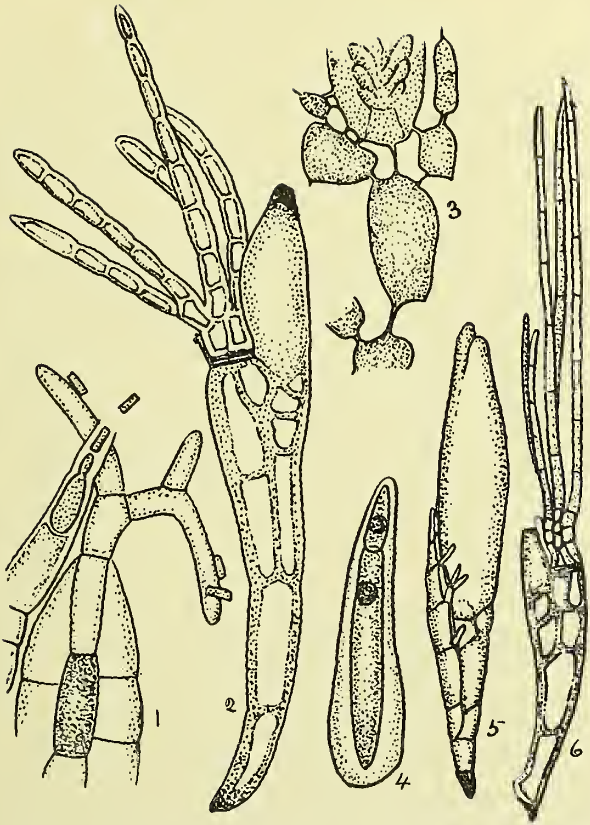

FIG. 28.—1, *Laboulbenia cristata*, young perithecium with antheridia above at the left. The darker axile cell the carpogonium, above it the trichophoric cell terminated by the trichogyne, on which are several antheridia; 2, *Laboulbenia Brachini*, elongate form with exceptionally simple appendages; 3, *Laboulbenia elongata*, portion of a specimen treated with potash and stained with eosin, slightly crushed so as to separate the basal cells without destroying the ascus mass and the inferior supporting cell. The protoplasmic portions of the cells only drawn to show the continuity between adjoining cells; 4, spore of same showing two nuclei; 5, *Sphaleromyces occidentalis*, mature individual; 6, *Laboulbenia Philonthi*. All highly mag. (After Thaxter.)

adhering to them. Afterwards the trichogyne soon withers and disappears. The non-motile antherozoids are minute cylindrical bodies, endogenous or exogenous in origin. Endogenous antherozoids, so far as is known, are confined to two aquatic genera. The antheridia are usually so placed that the antherozoids are liberated very near to, or actually upon, the trichogyne, to which they adhere. After fertilisation the carpogenic cell divides into several cells; some of these cells, the ascogenic cells, begin to bud, the buds developing directly into asci. The asci contain either four or eight spores, and deliquesce at an early stage as in many other Ascomycetes, liberating the spores in the perithecium, from which they escape at maturity. The perithecium originates from a cell placed below the ascogonium. The behaviour of the nuclei during fertilisation and afterwards is not known.

The mode of fertilisation described above agrees in all essential features with that presented by the Florideae, and some Lichens. Similar trichogynes, more or less aborted, also occur in other groups of the Ascomycetes, as in *Xylaria*, *Poronia*, etc.

Blackman has described what he considers to be a process of fertilisation in the aecidium of *Phragmidium violaceum*, one of the Uredineae. From the mass of vegetative hyphae constituting the first evidence of an aecidium, those cells immediately beneath the epidermis increase in size and become divided by a transverse wall, each cell containing a single nucleus. The upper cell is a sterile cell and soon disappears. The lower cell becomes binucleate, and eventually produces a series of binucleate aecidiospore mother-cells. The problem as to how the lower or fertile cell became binucleate was solved by the discovery of a number of cases in which a nucleus was actually found passing into the fertile cell from one of the smaller cells of the mycelium at its base. The migrating nucleus passes from a cell situated below the fertile cell, and sometimes passes into the fertile cell immediately above it, or more frequently passes into a fertile cell belonging to another row, situated by its side. The migrating nucleus is reduced to a thin thread during the process, and neither before nor after its passage could a pit in the wall be observed. Although two nuclei are usually eventually present in the fertile cell, three are sometimes to be seen, in fact three nuclei are nearly always to be found in a few of the fertile cells of each aecidium. In one case a fertile cell containing four nuclei was observed. Whether this number of nuclei was due to the migration of more than one nucleus into the fertile cell, or to division of the usual two nuclei, was not determined.

Fusion does not take place in the fertile cell between the two or more nuclei present. These divide by what is termed conjugate division, and when two nuclei are present in the fertile cell, two nuclei are present in each aecidiospore, and three when the fertile cell contains three nuclei. Nuclear fusion takes place at a later stage of development between the pairs of nuclei found in the teleutospores.

It is considered that throughout the group the aecidium must be looked upon as a sorus of reduced female organs. Considering the spermogonia and aecidia as male and female reproductive organs respectively, it is evident that those Uredineae which possess an aecidial stage exhibit a well-marked alternation of generations. The sexual generation—spermatia and aecidia—having single nuclei, with two chromatin masses on division ; the asexual generation—uredospores and teleutospores—having paired nuclei, with four chromatin masses on division. The change from gametophyte to sporophyte occurs in the aecidium, and the transition from sporophyte to gametophyte in the teleutospore.

It has already been stated that Blackman observed what he considers to represent a reduced form of trichogyne present in the aecidium. This organ is represented by what has been here spoken of as the sterile terminal cell, surmounting the fertile cell in the aecidium. The spermatia are considered as male organs, at present functionless. The presence of these rudimentary organs is considered as indicating an affinity between the Uredineae and the Florideae.

Following Blackman, Christman, an American investigator, has paid special attention to what he terms sexual reproduction in the rusts. The species investigated were *Phragmidium speciosum* and *Cacoma nitens*. Blackman's observations are, on the whole, corroborated, and the author states his opinion that the discoveries made establish the existence of true sexual cell fusions in the rusts, and that the fusion of nuclei in the teleutospore is not of a sexual nature, but has wholly to do with the reduction of the number of chromosomes. The behaviour of what Blackman terms the fertile cells in a sorus, that are compacted vertically to the surface of the leaf, is as follows. These approach in pairs until portions of two contiguous walls are in contact, and at this point of contact a pore is formed by the solution of the cell-walls, and the protoplasts are brought into contact. The two nuclei pass to the apical portion of the conjugated cell and divide simultaneously. Two of the daughter-nuclei return to the base of the conjugated cell, whereas its apical portion containing two nuclei is cut off by a transverse wall, and constitutes the first aecidiospore mother-cell. This cell at once divides into two unequal cells, the aecidiospore and the small intercalary cell. After one aecidiospore has been formed, the nuclei in the basal conjugated portion again divide, another aecidiospore is cut off, and by a repetition of this process a chain of aecidiospores is formed in basipetal succession. Probably when a greater number of species are examined, apparent discrepancies as to the method of forming a binucleate cell, as described by Blackman and Christman respectively, may be explained.

Dangeard's ideas respecting sexuality in the higher fungi are as follows. The higher fungi consist of two principal branches, Basidiomycetes and Ascomycetes, in which sexual reproduction is uniform throughout. The Basidiomycetes are subdivided into the Ustilagineae, Uredineae, Protobasidiomycetes, and Basidiomycetes.

In the Ustilagineae the young cells of the mycelium are binucleate; older cells may contain more than two nuclei. The formation of asexual conidia reduces the cells to a uninucleate condition for the time being. In sexual reproduction the cells become swollen or give off vesicular branches; the two nuclei of each cell are of different origin. Each swollen cell with its two nuclei should be considered as a gametangium containing two uninucleate gametes, each nucleus having lost the power of dividing as in an ordinary gamete. The two gametes combine to form one by the fusion of the two nuclei. The reserve material accumulated in the swollen cell constitutes an oospore which increases in size, and becomes surrounded by a thick membrane consisting of an epispore and an endospore.

On germination the oospore gives origin to a stout promycelium-tube containing the protoplasm and the sexual nucleus of the oospore. This nucleus by two successive karyokinetic divisions forms four nuclei. These four nuclei

FIG. 29.—*Urocystis occulta*, one of the Ustilagineae. 1, upper part of a rye plant attached by the fungus; 2, clusters of spores, one of which has germinated and produced a cluster of secondary spores; 3, a spore that has germinated and produced secondary spores, two of which have produced tertiary spores, *a*. Fig. 1, reduced; the others mag.

are isolated by septa, and each of the cells produces exogenous spores, or sporidia, as they are usually called. In some genera the sexual nucleus undergoes three successive bipartitions in the non-septate promycelium, and the eight nuclei formed pass in order into the sporidia that are formed by budding, at the apex of the promycelium.

The promycelium is none other than an ordinary sporogonium; it is in its interior that the sexual nucleus having $2n$ chromosomes resulting from fusion in the gametangium, reverts to its normal structure, represented by n chromosomes. This necessary reduction, observed by Sappin-Trouffy in Uredines, is without doubt produced in the same organ in all the Basidiomycetes.

The mode of formation of the oospore in the Ustilagineae does not imply changes in the protoplasm; this act is, however, not much retarded, but takes place on the germination of the oospore, through the frequent anastomosing of the cells of the promycelium and of the sporidia.

In the Uredineae the cells bearing ordinary conidia or spermatia are uninucleate, all other cells of the mycelium are binucleate; these nuclei divide simultaneously at the same level, and the spindles are parallel to the axis; thus it results that the median septum isolates for each new cell two nuclei whose relationship to each other becomes more and more distant. From this method, passing on from the stroma of the aecidium, it can be conceived how different in origin must be the pairs of sexual nuclei present in the teleutospore. The gametangia are rarely isolated, usually grouped in pairs, sometimes three, according to the genera, at the apex of a pedicel, and collectively known as teleutospores. In each gametangium the oospore is formed as in the Ustilagineae; the two nuclei fuse, and the oospore passes into a resting-stage, protected by a double membrane.

Each oospore, on germination, produces a promycelium in which the sexual nucleus undergoes a double karyokinetic division. From the prophase of the first division, the sexual nucleus, which contained $2n$ chromosomes due to fusion in the gametangium, never shows more than n; it has thus returned to the normal structure. The promycelium becomes divided into four cells, each containing a nucleus, and each cell by budding produces a single spore or conidium.

If the grouping of the gametangia into a teleutospore is abstracted, it is observed that the sexual reproduction in the Uredineae is entirely in agreement with that of the Ustilagineae.

The Protobasidiomycetes only differ from the Uredineae in the oospore germinating at once without a resting-stage. Almost immediately after fertilisation the oospore [basidium] increases in length, the sexual nucleus undergoes two bipartitions, and the four nuclei are separated by cross-walls. The promycelium stage occurs within the oospore instead of externally, as in the Uredineae; each of the four cells gives origin to a spore. In this family the septa are parallel to the axis, or perpendicular, according to the genera.

The Basidiomycetes are the most elevated of the series. The cells of the mycelium generally contain two nuclei; the division preceding the separation of the young basidia agrees with that in the Uredineae. The young basidia represent the gametangia of the preceding groups, and fertilisation is also effected under similar conditions. The oospore germinates immediately; the sexual nucleus divides indirectly, forming four new nuclei; this division is not followed by the formation of cross-walls, all trace of a promycelium has disappeared, and four spores are produced directly on the basidium.

From the Uredineae to the Basidiomycetes proper the progressive reduction of the promycelium to its entire disappearance is complete, and all the other phenomena correspond with absolute exactitude.

In the Ustilagineae the mixture of different protoplasm is effected by the anastomosing of the cells of the promycelium and of the sporidia. In the other groups there is not the same opportunity, yet anastomosing of the hyphae is of frequent occurrence, but produced at different stages of development, and more or less removed from the period of germination of the oospore.

In the Ascomycetes the phenomena of reproduction are simple, as in the Basidiomycetes. There is not the same uniformity in the structure of the mycelium. The cells are uninucleate or multinucleate; in some species there are more than thirty nuclei in a cell, and variations exist in the number of nuclei present in different cells of the same mycelium. When two nuclei are present in a cell, as in *Exoascus*, the different origin of the sexual nuclei results from a simultaneous and parallel division, as in the Uredineae. Most frequently another method is followed; the extremity of a filament becomes recurved against the cell below it, the nuclei of these two cells divide, then two septa isolate a gametangium containing the two median nuclei, which are of different origin. Sometimes the gametangium is formed from two contiguous uninucleate cells whose contents fuse. The gametangium contains two gametes, as in the Basidiomycetes; after fusion of the nuclei the oospore is formed.

The germination of this oospore is in every respect comparable with that of the Basidiomycetes, and takes place immediately. The oospore grows into the ascus, in which the sexual nucleus usually undergoes three successive karyokinetic divisions, thus forming eight nuclei, corresponding to the usual number of spores present in an ascus.

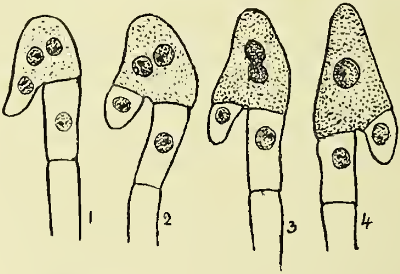

FIG. 30.—Stages showing the formation of an ascus from the apex of an ascogenous hypha in *Peziza badia*. 1, the terminal cell forming a hook, and containing three nuclei; 2, the terminal portion of the hook containing one nucleus cut off by a septum, the penultimate cell containing two nuclei is the young ascus; 3, the two nuclei in the young ascus commencing to fuse; 4, young ascus elongating and showing complete fusion of its two nuclei. This sequence illustrates the development of a binucleate oospore according to Dangeard's view. All highly mag.

The mode of formation of spores is slightly different; in the Basidiomycetes they are exogenous, in the Ascomycetes they are produced in the interior of the ascus, or endogenous.

Such are the broad outlines of Dangeard's conception of sexual reproduction in the higher fungi, which it must be admitted is concise and logical, and may possibly represent a new conception of sexuality intended eventually to replace the more primitive form, which, as already stated, is undoubtedly on the decline.

Although the origin of the ascus from the binucleate, penultimate cell of an ascogenous hypha is very frequent, it is not constant, as indicated by Faull, who has quite recently investigated the subject, and summarises his observations as follows:—

1. The asci bud out from the penultimate cells of the ascogenous hyphae in some forms, in others from the terminal cells, and in a few species apparently from any cell.

2. In every case that was definitely determined, the uninucleated stage is preceded by a fusion of two nuclei within the ascus. The conjugating elements, though not sisters, may sometimes be the daughters of sister nuclei.

3. The age and development of the asci at the time of fusion vary considerably in different species, and to some extent, though within narrower limits, in the same plant.

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ASEXUAL REPRODUCTION

It will have been gathered from preceding remarks that sexual reproduction is a factor of some uncertainty; however, for convenience, all spores that are the product of proved fertilisation, also spores produced by structures homologous with those where fertilisation is evident, but in which the sexual organs are now rudimentary, will be included under this heading, and left out of discussion in the present chapter. There still remain a great variety of reproductive bodies of undoubted asexual origin, respectively called spores, conidia, etc. All these and others are produced on specialised portions of the mycelium, whereas a second batch of reproductive bodies are purely vegetative in origin, as sclerotia, gemmae, etc.

We will commence with those forms borne on specialised portions of the fungus, and at the outset are confronted with the difficulty of clearly defining the various terms used to distinguish the different kinds, owing to the vague manner in which they have been designated by different authors.

Basidiospores are characteristic of the Basidiomycetes and the Protobasidiomycetes, and in these instances are exogenous in origin, being borne on basidia. In systematic works basidiospores are almost invariably called spores. The reproductive bodies produced in the asexual sporangia of the Mucorineae are called spores.

Typical conidia are the asexual summer form of fruit, borne on conidiophores in the Ascomycetes. As a rule, the production of conidia commences early in the season, and lasts through the summer. These bodies are produced in immense numbers and in quick succession, are readily dispersed by wind, insects, birds, mammals, and other agents, and are capable of germination the moment they are mature. Their special function is that of extending the geographical area of the species producing them. In the case of parasitic species the outbreak of an epidemic is caused by the rapid production and dispersion of the

FIG. 31.—*Pholiota adiposa*, a typical Basidiomycete. 1, a cluster of sporophores, *a*, pileus. *b*, stem ; 2, section of pileus, *a*, *a*, lamellae or gills, *b*, *b*, the secondary veil ; 3, spores, technically conidia, as they are of asexual origin. Figs. 1 and 2, half nat. size ; fig. 3, highly mag.

conidial form of reproduction. The ascigerous form of fruit, which usually enters on a period of rest before it is capable of germination, is more especially for the purpose of continuing the species in time; it tides over that period when conditions are unfavourable for the continued growth of the individual.

Zoospores, produced by many of the Phycomycetes, perform the same function for species as that stated for conidia. It may be noted, however, that some zoospores are also produced in fruit of sexual origin, as in *Cystopus*.

Oidia are very minute conidia-like reproductive bodies usually produced in chains, and terminal on the first formed tubes of a germinating spore. Our knowledge of these bodies is mainly due to the researches of Brefeld. Biffen has shown that in *Collybia velutipes*, the hyphae produced by germinating spores soon break up into oidia-chains. When the hyphae of this fungus has formed a small mycelium in the vessels and tracheids of a piece of wood, it becomes broken up into oidia which germinate quickly, and thus the wood is permeated by a large quantity of mycelium in a short time.

I have observed the formation of long chains of oidia terminating the germ-tubes of conidia of *Botrytis cinerea*.

In the host of forms included under 'fungi imperfecti' the reproductive bodies should properly be called conidia, although the term spore is common in systematic works. In some systematic works the term spore is applied to all reproductive bodies of exogenous origin, as basidiospores, etc., and the term sporidia to all spores of endogenous origin, as ascospores, etc.

As an exception to the general statement that conidia

Fig. 32.—*Rosellinia radiciperda*, a typical Ascomycete showing conidial and ascigerous forms of fruit. 1, ascigerous stage of the fungus showing

[*Description continued on p.* 103.

have a thin wall, and germinate once, may be mentioned azygospores and chlamydospores.

Both these become surrounded by a thick cell-wall, and are true resting-spores, that is, they require to remain for some time in a dormant condition before they are capable of germination, yet both are asexual in origin. Azygospores are found in some species of the Mucorineae; they are formed on the same plan as true zygospores, but no fertilisation takes place. Either the two gametes do not come in contact, or only a single gamete is present. These solitary gametes increase in size, develop a thick cell-wall, undergo a period of rest, and germinate after the manner of zygospores.

Chlamydospores are also thick-walled resting-spores, produced interstitially on vegetative mycelium, in certain Mucorineae and Agarics; rarely on short lateral branches, as in Hypomyces, belonging to the Ascomycetes.

Sclerotia are the most general of purely vegetative reproductive bodies. They consist of more or less globose

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the sexual fruit or perithecia; 2, perithecia or sexual fruit on a larger scale, showing the papilla at the apex, which is perforated for the escape of the spores; 3, section of perithecium, showing the wall to consist of two layers; 4, an ascus containing eight spores, also two paraphyses; 5, tip of an ascus after treatment with iodine, showing the arrangement for effecting the opening of the ascus, due to expansion of the dark portion, so as to admit of the escape of the spores; 6, ascospores, one of which is germinating; 7, brown mycelium with swellings at intervals; this peculiar swelling just below the septum is very characteristic of two or three allied parisitic species of Rosellinia; 8, a black sclerotium belonging to the fungus, bursting through the cortex of a root, and bearing several clusters of conidiophores bearing conidia; 9, a single conidiophore on a larger scale, showing the mode of branching: conidia are borne at the tips of the branchlets; 10, free conidia; 11, a pycnidium, or second form of conidial fruit, in which the conidia or stylospores are produced in a conceptacle; 12, stylospores. Fig. 1, nat. size; the remainder highly mag.

masses of hyphae, formed from the mycelium. When fully developed they become free from the mycelium, and

FIG. 33.—*Lentinus cyathus*, an agaric springing from a sclerotium; the latter shown in section. One-sixth nat. size.

contain an ample supply of reserve material. After a period of rest they produce sporophores, as in *Peziza* *tuberosa*, *Lentinus cyathus*, and *Polyporus mylittae*; or conidiophores as in a species of *Botrytis*, the sclerotia of which are common on the dead stems of umbellifers. When dry, sclerotia are very hard and compact, but examination shows that the entire substance consists of densely interwoven hyphae, white in the interior, and covered with a rind of thick-walled brown or blackish isodiametric cells. Sclerotia vary much in size; those of *Collybia tuberosa* and species of *Typhula* rarely exceeding two mm. in diameter, whereas a sclerotium of *Polyporus mylittae* now in my possession, measures eight inches in

FIG. 34.—*Sclerotinia sclerotiorum*, a sclerotia-forming fungus belonging to the Ascomycetes. 1, portion of a chrysanthemum stem containing black sclerotia of the fungus in the pith cavity; 2, sclerotium bearing five ascigerous fruiting bodies; 3, an ascus with spores, by its side is a paraphysis. Figs. 1 and 2, nat. size; fig. 3, highly mag.

diameter, and weighs four pounds in the dry condition. Many kinds of small sclerotia are formed in the tissues of plants that have been attacked by the fungus producing the sclerotia, and in the case of parasitic species, the primary infection of a crop is often due to the presence of sclerotia that have been carried with manure to the land. De Bary gives a detailed account of the structure of sclerotia, also of rhizomorphs, which functionally agree with sclerotia, from which they differ in assuming an elongated, cord-like form. The long, black, anastomosing rhizomorphs of *Agaricus melleus* are well known.

Both sclerotia and rhizomorphs were at one time considered as true species, and called *Sclerotium* and *Rhizomphora* respectively.

Buds or gemmae are formed under certain conditions of growth of the mycelium of various species belonging to the Mucorineae and others. Portions of hyphae or conidiophores rich in protoplasm become divided into short cells by the formation of cross-walls; such cells often become thick-walled, enter into a resting-stage, and afterwards produce ordinary mycelium. In other instances the walls of these modified hyphal cells remain thin, and reproduce themselves by budding from all parts of the surface, after the fashion of yeasts or *Saccharomyces*. Such buds give origin to mycelium and produce the typical fruit of the species from which they originated, when placed under favourable conditions.

When these budding forms of *Mucor* are produced in abundance, they possess the power of setting up alcoholic fermentation, and this fact led to the erroneous belief that the *Saccharomyces* were not entities, but produced under certain conditions by *Mucors* and other fungi.

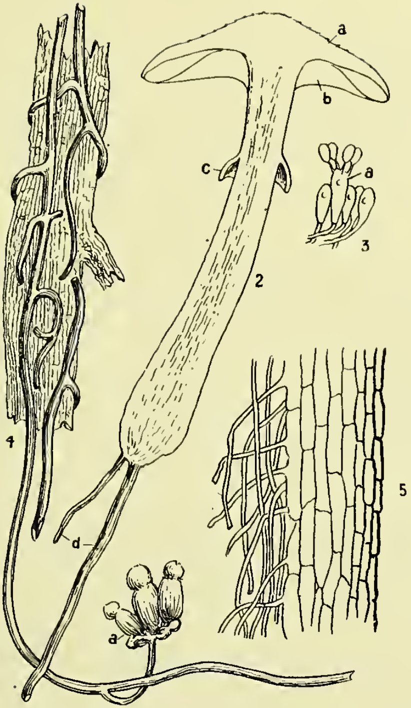

FIG. 35.—*Armillaria mellea*, a Basidiomycete forming rhizomorphs. 2, section through a sporophore, *a*, pileus; *b*, lamellae or gills; *c*, ring or annulus; *d*, black, cord-like strands of compacted mycelium or rhizomorphs; 3, portion of hymenium or spore-bearing surface of a gill, *a*, basidium bearing four spores; 4, portion of a root of a tree with branching rhizomorphs of the fungus surrounding it; at *a*, a cluster of young sporocarps are springing from a rhizomorph; 5, section through a rhizomorph, showing the thick-walled hyphae forming the rind, and the colourless thin-walled hyphae of the central portion. Figs. 2 and 4, nat. size; figs. 3 and 5, mag.

I have frequently observed that from the broken ends of conidiophores of *Cladosporium*, *Helminthosporium*, and other moulds, when present in a hanging-drop culture, a new growth started which developed into a branch bearing a head of concatenate conidia, smaller and different in other respects from the normal conidia of the species under observation.

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LIBERATION OF SPORES AND CONIDIA.

In those groups of the Phycomycetes, as the Saprolegniaceae, Chytrideae, and Peronosporeae, where aquatic zoospores are formed, a specialised portion of the wall of the zoosporangium, usually situated at its apex, becomes soluble in water when the zoospores are ready for liberation. At this period water is absorbed, and a hyaline layer lining the wall commences to swell; as the wall of the zoosporangium is comparatively rigid, the swollen contents expel the zoospores, through the specialised apical opening, into the surrounding water.

In most members of the Mucorineae the upper portion of the sporangial wall, which is usually coated externally with a thin coating formed of minute particles of oxalate of lime, becomes soluble in water at maturity, and the absorption of water by the intersporal substance causes the liberation of the spores. In *Pilobolus*, the species of which grow on dung, the entire sporangium is ejected at maturity to a considerable distance, and adheres firmly to the substance it alights upon. If this substance happens to be grass which is afterwards eaten by some animal, the spores germinate in the intestines, and again produce fruit on the dung.

Several different methods of spore ejection are met with in the Ascomycetes. In many instances the ascus elongates considerably, sometimes to three or four times its previous length, as a preliminary to the emission of its spores. The ascus always remains fixed at the base, and does not break away from its point of attachment, and become pushed upwards by younger asci, as has been stated. The name *Ascobolus* was given to a genus on the strength of this erroneous idea. In many species belonging to the Pyrenomycetes, where the fruit-case or perithecium is furnished with a minute pore at the apex, through which the spores escape, the asci in the order of maturity elongate until the apex of the ascus reaches the pore, when the contained spores are expelled in successive order. After the emission of the spores, the ascus retracts and undergoes dissolution. In some species of *Chaetomium*, *Melanospora*, *Spumatoria*, etc., the asci become resolved into mucilage when the spores are mature. This mucilage increases enormously in volume by the absorption of water, and oozes out of the mouth of the perithecium, carrying the spores along with it, the two often forming a ball or long tendril-like mass at the mouth of the perithecium.

In other groups of the Pyrenomycetes, as the Perisporieae, Nectrioidae, etc., the perithecium is not provided with an aperture for the escape of the spores; their liberation in such instances being effected by rupture of the perithecial wall, caused by the swelling of mucilage.

In the Discomycetes, where the numerous asci are placed vertically and closely packed, their apices, along with the tips of the paraphyses, forming the surface of the cup, all the spores in an ascus are ejected simultaneously. In *Ascobolus* the spores are individually surrounded by a colourless layer of mucilage, or the whole of the spores in an ascus are bound together by mucilage, as in *Saccobolus*. Such spores are ejected with considerable force, and become firmly fixed to the substance on which they alight, by the mucilage which sets hard and is insoluble in water after exposure to the air. Those spore-masses that alight on grass or other herbage eaten by animals, either in a living or dried condition, germinate in the alimentary tract, and produce fruit on the dung.

In other species, where wind is the dispersing agent, the spores are liberated in clouds at intervals. This process, which is termed puffing, is due to the simultaneous discharge of the spores from numerous asci at the same moment. Various species of *Peziza*, *Helvella*, and *Bulgaria* exhibit this phenomenon. De Bary pointed out that puffing does not occur when the fungi are growing in a very damp and still atmosphere, as under a bell-jar; but that puffing commences as soon as such fungi are removed into a dry atmosphere. This is considered to be due to the sudden loss of water altering the state of tension in each ascus, and not to shrinkage and contraction of the entire hymenium. This is probably the true explanation of the phenomenon, as I have observed that puffing can be brought about in *Peziza vesiculosa* by concentrating the sun's rays for a moment on the hymenium by means of a pocket-lens.

In the Uredineae the chains of aecidiospores consist of alternating cells which become spores, and of small sterile cells which eventually deliquesce, setting free the spores as a powdery mass. Magnin states that in *Cystopus candidus* and allied species, the liberation of the conidia is due to the presence of a ring of callus which eventually becomes soluble in water. Woronin has described an elaborate arrangement for effecting the breaking up of the long chains of conidia belonging to species of *Sclerotina*. This apparatus, which alternates with the conidia in the chain, is termed a disjunctor.

FIG. 36.—*Peziza vesiculosa*, a typical ascigerous fungus belonging to the Discomycetes, which exhibits the peculiarity of puffing out the spores in clouds from the asci. Nat. size.

In the Hymenomycetes the mature spore is cut off from the apex of its sterigma by a transverse wall. The sterigma retains its parietal protoplasm after the spore is cut off, and its elastic wall continues to stretch as the tension due to the accumulation of water increases. When the tension reaches a certain point, the wall of the sterigma ruptures in a circular manner just below the septum at its apex; the elastic wall of the sterigma instantly contracts and forces its contained water to strike the apical transverse wall, which is thus thrown off along with the spore seated upon it.

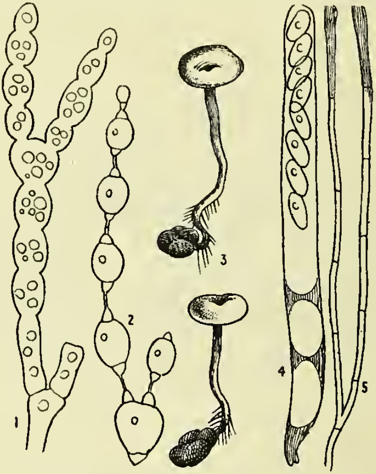

FIG. 37.—*Sclerotinia urnula*, a Discomycete, the conidia of which are liberated by 'disjunctors.' 1, chain of conidia in a young stage; 2, chain of conidia at maturity, the narrow necks or disjunctors deliquesce and liberate the conidia; 3, ascophores springing from mummified berries of *Vaccinium* filled with mycelium, forming a sclerotium; 4, ascus containing eight spores; 5, paraphyses. Fig 3, nat. size; the remainder highly mag.

If the pileus of a white-spored Agaric is placed gills downwards, and supported so that it rests about an inch above a sheet of black paper, and then covered with a bell-jar to prevent currents of air, it will be observed that when the spores are shed, they cover a circle considerably larger than that of the diameter of the pileus. This has been considered as evidence that the spores of Agarics are abjected or propelled to an appreciable distance. I have not been able to satisfy myself on this point; the difference between the temperature of the pileus and that of the enclosed air in the bell-jar might account for the diffusion of spores beyond the periphery of the pileus.

In *Sphaerobolus stellatus*, one of the Gasteromycetes, the entire inner peridium, which is about the size of a pin's head, is forcibly ejected, due to unequal tension of the different layers of the outer peridium. I once had a considerable quantity of this fungus under observation for some weeks. It was covered by a bell-jar twelve inches in diameter and eighteen inches high, and the inside of the upper half of the jar was studded with the minute peridia of the *Sphaerobolus*, which are covered with mucilage and remain fixed to the object they strike. When a peridium struck the glass, it could be heard in every part of the room. There is also a very audible sound when the outer peridium cracks to eject the spore-mass. There is obviously a slip somewhere in De Bary's statement, that in favourable cases the inner peridium of *Sphaerobolus* is shot to a distance of more than a millimetre. Perhaps 'a metre' was intended to be written.

Consult the chapter on 'Dispersion of Spores,' which to some extent covers the present chapter.

De Bary, *Fungi, Mycetozoa, and Bacteria* (Engl. ed.), pp. 89, 328.

Magnin, *Compt. Rend.*, 1891, pp. 176, 232.

Massee and Salmon, *Ann. Bot.* 5, p. 313 (1901).

Woronin, *Mém. de l'Acad. Imp. St. Petersb.*, ser. 7, 36.

DISPERSION OF SPORES AND CONIDIA

In the Basidiomycetes and the Ascomycetes wind is the most general agent in dispersing spores. Voglino has shown that slugs eat fleshy agarics, especially the hymenium, and spores commence to germinate in the

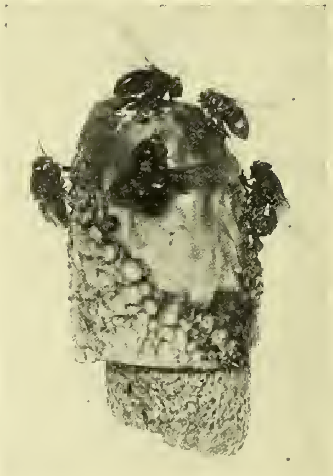

FIG. 38.—Hymenium of *Phallus impudicus* partly covered with olive-green mucus, in which the very minute spores are embedded. Several flies are present devouring the mucus. Nat. size.

intestine. Spores that refused to germinate in many media germinated readily in the liquid found in the digestive tract of a slug, and formed a strong mycelium. This author placed all slugs found feeding on fungi in an enclosed space of ground, and the following season observed many more species of agarics in this enclosed space than in the surrounding part. This was considered to be due to the facility for germination of the spores after having passed through the alimentary canal. Toads eat slugs; and spores, especially of species of *Russula*, have been found germinating in the intestinal canal; hence toads assist indirectly in the distribution of fungus spores.

Flies are also known to be active agents in this direction. In *Phallus impudicus* the strong-smelling green slime in which the very minute spores are embedded contains, according to Rathay and Haas, three forms of sugar: levulose, dextrose, and another intermediate between dextrose and gum. This fetid slime is greedily eaten by flies, and Fulton has proved that the spores of *Phallus* are transported in myriads by adhering to their feet and proboscides. He also showed that spores that had passed through the digestive system of flies germinated and produced the characteristic mycelial strands of *Phallus*.

This mode of spore dispersion is true of all the members of the Phalloideae, which are most abundant in tropical and subtropical regions. The hymenial portion of the sporophore is in many instances brightly coloured, usually red; there is equally constant, a very strong, penetrating smell, and a gluten in which the spores are embedded, containing substances serving as food for flies. Some species emit a phosphorescent light at night, which attracts moths. It is interesting to note that smell and colour, which assist in securing the fertilisation of some flowering plants, also assist in effecting the dispersion of spores in the Phalloideae.

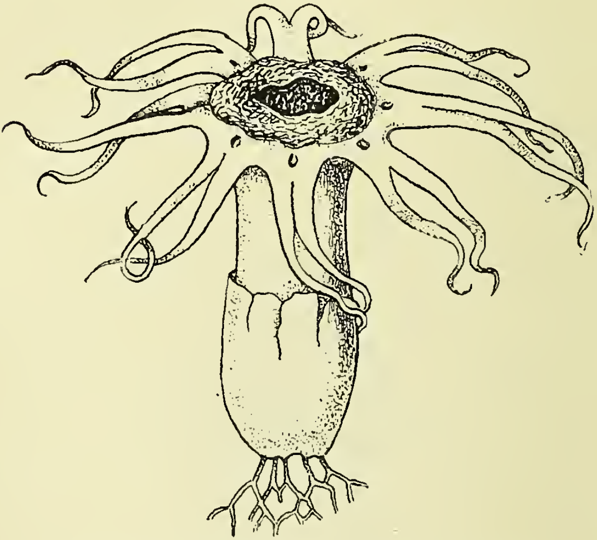

FIG. 39.—*Aseröe ruba*, an insect attracting fungus belonging to the Phalloideae. The stem and the sheathing volva at the base, which originally enclosed the whole plant, are white. The spreading rays, which are attractive on account of their brilliant crimson colour, also serve as a landing-stage for insects, from which they can devour the dark, central, slimy, sweet substance containing the spores. Two-thirds nat. size.

Minute spores or conidia, embedded in mucus containing sugar, belonging to other groups of fungi, are also distributed by flies, as the conidia of Ergot.

Many species of subterranean fungi, as truffles, etc., are eaten by rodents, and probably the strong smell possessed

FIG. 40.—*Claviceps purpurea*, or ergot. 1, ergot on rye-grass; 2, ergot on rye: the black, horn-like bodies are stromata or sclerotia of the fungus, and bear the conidial form of fruit; 3, portion of conidial form of fruit produced on a stroma: the conidia are mixed with a sweet substance attractive to flies; 4, a stroma bearing the stalked ascigerous form of fruit, after lying on the ground throughout the winter; 5, head or fertile portion of ascigerous fruit, showing the warted surface due to the

[*Description continued on p.* 118.

by such species when mature, serves to guide the animals to their whereabouts, and thus the spores are disseminated.

Spores are often dispersed by slugs and snails, by crawling alternatively over diseased and healthy parts of plants. Mites, flies, birds, mice, etc., carry spores adhering to their bodies, from one place to another; and probably are frequently the unconscious cause of a new infection, or the rapid spread of an epidemic due to fungi.

In one instance I was able to prove that a serious outbreak of disease caused by a fungus originated in the injured plants being inoculated by spores that had been blown into an open rain-water tank, the water from this tank being used for spraying. Consult the chapter on 'Liberation of Spores and Conidia,' in connection with this subject.

Fulton, *Ann. Bot.*, 3, p. 213 (1899).

Rathay and Haas, *Nat. Akad. d. Wissensch.*, 58, p. 18 (1883).

Voglino, *Nuovo Giorn. Bot. Ital.*, 1895, p. 181.

Falck, 'Die Sporenverbreitung bei den Basidiomyceten u. der biologische Wert der Basidie,' in Cohn's *Beitr. Biol. d. Pflanzen* (1904).

MINERAL FOOD OF FUNGI

According to Errera the elements necessary for organic life have low atomic weights, Fe. 56 being the highest.

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projecting mouths of the perithecia: the section shows the numerous perithecia sunk in the fleshy stroma; 6, an ascus containing eight needle-shaped spores; 7, a single spore. Figs. 1 and 2, nat. size; the remainder mag.

This is said to be due to their higher specific heat; thus water has the highest specific heat of all substances, and consequently it can diminish the effects of rapidly changing temperatures upon life.

The physiological rôle of mineral nutrients is not known in most instances, but only the experimental proof that certain substances have a more or less marked effect on growth.

Potassium salts are necessary in most fungi for the production of protein, even when sugar is present.

Magnesium salts are also indispensable, but a mere trace is sufficient when the nutrient medium has an acid reaction.

Molisch, in studying the action of iron on the higher plants, also observed that when salts of iron were added to the nutrient medium of *Aspergillus niger*, growth was much more luxuriant. He therefore concluded that iron was as essential to fungi as to the higher plants. Wehmer has verified Molisch's statement, but considers his conclusion as too general, as it was observed that if nitrate of ammonia is replaced by nitrate of potash, the presence or absence of iron makes no appreciable difference to the vigour of growth,

Günther states that even in the case of suitable salts, a diminution of growth takes place as the salts become more concentrated. A combination of salts beneficial to fungi is a salt of potassium and of magnesium, along with a compound containing sulphur and another containing phosphorus.

Rubidium can replace potassium in the case of *Botrytis cinerea*, but not in that of *Rhizopus nigricans*.

Salts of copper in exceedingly minute proportions favours the growth of fungi, whereas larger proportions of the same salts act as a poison.

Günther, *Beitr. z. mineralischen Nährung d. Pilze*; Inaug. Diss., *Erlangen*, 1897.

Molisch, *Die Pflanzen: ihre Beziehungen z. Eisen*; Jena, 1892.

Wehmer, *Beitr. z. Kennt. einheimischer Pilze*; Jena, 1895.

EFFECT OF LIGHT AND DARKNESS RESPECTIVELY ON THE GROWTH OF FUNGI

It is not possible to formulate laws as to the action of light on fungi. The photochemically active rays of the spectrum—the blue end—destroy bacteria, and according to Klein these same rays prevent the formation of conidia in *Botrytis cinerea*, which can only be produced in darkness. Ferguson's experiments also tend to show that light has an inhibitory effect on the germination of the spores of *Agaricus campestris*. On the other hand, Brefeld has shown that light is necessary for the perfect development of the sporophore in *Pilobolus*, and in species of *Coprinus*, both of which become abnormal and etiolated in darkness.

It is well known that many kinds of fungi growing on wood in mines and other dark places develop abnormally, and often assume very fantastic forms.

Lentinus tigrinus, a large agaric, when introduced into mines on timber, undergoes strange modifications; in place of a normal pileus, several branches, more or less resembling stags' horns, are formed; these are usually quite sterile, or occasionally traces of rudimentary gills are present. *Merulius lacrymans*, or 'dry rot,' also often develops monstrous forms when growing in dark places, whereas when developed under normal conditions, the entire plant forms a thickish crust attached at every point to the matrix upon which it is growing. Biffen finds that *Agaricus velutipes*, when grown as a pure culture, assumes abnormal forms in darkness, the pileus being arrested. This is perhaps not remarkable, my own experience being that the sporophores of all fungi, excepting conidial forms, are always more or less abnormal when grown as pure cultures, even under the most favourable conditions.

Biffen, *Journ. Linn. Soc.*, 34, p. 147 (1898).

Brefeld, *Unters. über Schimmelp.*, *Heft* 3, p. 87, and *Heft* 4, p. 76.

Ferguson, *U.S, Depart. Agric.*, *Bull.* No. 16 (1902).

Klein, *Bot. Ztg.*, 1855.

EFFECT OF LOW TEMPERATURE ON THE GERMINATION OF SPORES

Eriksson has shown that the capacity for germination is in some instances accelerated by exposure to cold. In *Aecidium berberidis* this was observed in seven out of twelve experiments when slightly cooled (not exceeding 0° C.); and in four out of five instances when strongly cooled (below 0° C.). On the other hand, an extremely low temperature was found to retard germination.

Chodat determined that the spores of *Mucor mucedo* do not benefit by exposure to very low temperatures (−70° to −110° C.). The fungus, however, when exposed to this low temperature for sixty hours, is not killed; the mycelium continues to grow, somewhat slower than at ordinary temperatures, and normal sporangia are formed. The author considers that as respiration is entirely suspended at this temperature, the theory that respiration is a necessary condition of vegetable life requires modification.

It is quite probable that spores will bear without injury a temperature much lower than indicated above, as Sir William Thiselton-Dyer has shown that the seeds of some flowering plants, *Brassica alba*, *Pisum sativum*, *Cucurbita Pepo*, *Mimulus moschatus*, *Triticum sativum* and *Hordeum vulgare*, were not in any way impaired by exposure to a temperature of − 250° C. for over an hour.

Chodat, *Bull. Herb. Boiss.*, p. 890 (1896).
„ *Bot. Centralbl.*, 70, p. 242 (1897).
Thiselton-Dyer, *Ann. Bot.*, 13, p. 559 (1899).
Eriksson, *Kgl. Land. Akad. Handl. Tidskr.*, 34, p. 216 (1895).

EFFECT OF MECHANICAL MOVEMENTS ON GROWTH

According to Russell, the form and size of fungus cells are but little influenced under constant agitation ; hyphae, however, are not formed freely. Such conditions greatly favour the increase in the number of cells, and consequently the amount of organic matter produced. The chief reason is considered to be more perfect aeration and the better conditions of nutrition.

Russell, *Bot. Gaz.*, 1892, p. 18.

RESPIRATION AND TRANSPIRATION

General conclusions based on experiments on the fruiting portions of fungi by Bonnier and Magnin are as follows :—

Respiration

1. Is augmented by an elevation of temperature, but there is no optimum.

2. Diffused light retards its intensity.

3. The most refrangible rays of light favour the process to the greatest degree.

4. Is accelerated by increase of moisture in the air.

5. The value of the ratio $\frac{CO_2}{O}$, carbonic acid given off, and of oxygen absorbed, is variable in different species, but is in general less than the unit. Fungi assimilate oxygen.

6. The ratio $\frac{CO_2}{O}$ is constant for a given species, and does not vary with the pressure.

7. This ratio is constant at all temperatures.

Transpiration

1. Is augmented by the elevation of temperature.

2. Diminishes as the amount of moisture in the air increases.

3. Is favoured by diffused light.

Kolkwitz, experimenting with *Penicillium*, and using the electric light instead of sunlight, observed that under these conditions respiration increased about ten per cent. This result was constant whether the fungus was young or old, in rich or poor nutrient media, or in an acid or alkaline substance.

Intramolecular respiration, or the liberation of carbonic acid in an atmosphere deprived of oxygen, takes place in some fungi, according to Diakanow; but only when the nutrient medium contains a fermentable substance.

Bonnier and Magnin, *Ann. Sci. Nat.*, ser. 6, 7, p. 210 (1884).

Diakanow, *Archiv. Slav. de Biologie*, 1886, p. 531; 1887, pp. 6, 31, and 121.

Kolkwitz, *Pringsh. Jahrb.*, 33, p. 128 (1899).

FIXATION OF FREE NITROGEN BY FUNGI

Ternetz has announced the discovery of a fungus in peaty soil which fixes the free nitrogen of the air. The mycelium is septate and branched. Pycnidia containing hyaline conidia are formed; these conidia are so very minute that they pass through thick filter-paper.

Ternetz, *Ber. d. deutsch. Bot. Ges.*, 22, 267 (1904).

ENZYMES AND FERMENTS

Enzymes are substances elaborated by living cells, and possess the property of effecting chemical changes in certain substances even after their removal from such cells; hence the action of an enzyme is purely chemical, as opposed to vital. If an enzyme is precipitated by alcohol, and afterwards properly prepared, the resulting precipitate, dissolved in water, produces exactly similar changes in a given substance to those effected by an extract obtained from living cells. Enzymes act by causing the molecules of insoluble substances to take up water, and to split up into simpler molecules of a different composition and soluble in water. There are no gaseous by-products.

According to Went the secretion of enzyme by *Monilia sitophila* is influenced by nutrition. Food rich in carbohydrates promotes the formation of the greatest amount of enzyme. The quantity of such food also exercises an influence, and an excessive quantity checks the secretion. This author does not accept the general opinion that the secretion of an enzyme indicates the lack of certain nutrients, or cell-starvation. Ward has shown that it is by means of a minute drop of enzyme, secreted by the tip of a hypha, that the latter is enabled to penetrate the walls of living cells of the host-plant. Biffen has demonstrated the presence of a fat destroying enzyme in a fungus, probably a species of *Nectria*. In this instance the enzyme acted by first emulsifying the fat of cocoa-nut endosperm, and then splitting it up into a fatty acid and glycerine.

Certain glucosides, as salicine, amygdaline, coniferine, and aesculine, are broken up by enzymes, and yield among other products glucose, a sugar that can be directly assimilated by fungi.

Wehmer founded a genus called *Citromyces* for certain fungi capable of changing carbo-hydrates into citric acid. The production of this acid is due in the first place to the oxidation of the carbo-hydrate, and is dependent on the presence of oxygen. The most favourable nutrient solution for its formation is a moderately strong solution of sugar.

Organic ferments agree with enzymes in being able to effect chemical changes in organic substances, but differ materially in the fact that such changes can only be induced under the influence of the living cells producing the ferment.

This amounts to stating that organic ferments are living cells, hence the assumption by Weisner, Pfeffer, and Noll, that alcoholic fermentation is identical with intramolecular respiration. In their action ferments differ from enzymes in splitting up complex organic compounds into several substances of a totally different and less complex nature than the original. During this process there is a liberation of gaseous by-products, carbon dioxide being almost constantly evolved.

Enzymes and ferments agree in one particular: neither body loses its individuality as is the case with an ordinary reagent, when causing a chemical change in a given body to which it is added.

Yeasts, or species of *Saccharomyces*, are characteristic ferments, liberating alcohol and carbon dioxide in varying proportions, depending on the particular kind of yeast, by acting on hydro-carbon compounds.

When a hydro-carbon is not present in the first instance, fermentation of a given substance is the joint result of two distinct organisms working in unison. Thus the yeast employed in the production of saké in China consists of an *Aspergillus* and a *Saccharomyces*. The former, by means of an enzyme, inverts the rice, and makes it accessible to the ferment furnished by the *Saccharomyces*. Ward has demonstrated that the so-called 'ginger-beer plant' is a compound of a Bacillus and a yeast, the work of both being necessary for the production of ginger-beer. It is further stated that a condition of mutualism or interdependence exists between these two organisms.

As opposed to the statement already made that fermentation depends on the presence of living cells, it may be well to note the statement by Büchner, who has separated from

Saccharomyces a product he calls zymase, which produces a characteristic and vigorous fermentation, independent of living protoplasm. It is considered probable, although not yet proved, that the yeast cells excrete zymase into the surrounding liquid, and consequently fermentation takes place outside and not inside living cells. In a later communication Büchner announces that he has obtained zymase from dead yeast.

Biffen, *Ann. Bot.*, 13, p. 363 (1899).

Büchner, *Ber. d. deutsch. Chem. Ges.*, 30, p. 117 (1897); *idem*, 33, p. 3307 (1900).

Ward, *Ann. Bot.*, 2, p. 319 (1889).

Wehner, *Comp. Rend.*, 117, p. 332 (1893).

Went, *Koninkl. Akad. van Wetensch. te Amsterdam*, Feb. 23, 1901, p. 489.

Bourquelot, *Bull. Soc. Myc. France*, 9, p. 189 (1893). This author mentions the occurrence of a ferment in *Aspergillus niger* capable of transforming trehalose into glucose.

Green, *The Soluble Ferments and Fermentation*, London, 1899. Contains full account of the enzymes occurring in Fungi.

Vines, 'The Proteases of Plants,' *Ann. Bot.*, 18, p. 289 (1904).

TOXIC EFFECTS OF DIFFERENT SUBSTANCES ON FUNGI

According to Clark, fungi in general are much more resistant to deleterious agents than are the higher plants.

A concentration of from two to four hundred times the strength fatal to the higher plants is necessary to inhibit the germination of fungus spores when mineral acids are used. The protoplasm is much more susceptible to the action of such agents during the conidial stage than at any other period of the life-cycle.

On the other hand, formaldehyde, which is non-toxic to the higher animals, is very deadly in its action on fungi, being surpassed only by mercury, silver, and two chromates, out of the compounds experimented with by Clark. The fact of formaldehyde being both a reducing and an oxydising agent, coupled with its great instability, may account for its extreme toxic effect on fungi. As represented by equimolecular formulae, the toxicity of formaldehyde is as follows: $\frac{n}{512}$ proved fatal to *Aspergillus* and *Penicillium*; $\frac{n}{2048}$ to *Sterigmatocystis* and *Botrytis*; whereas $\frac{n}{8192}$ proved fatal to *Oedocephalum.*

As contrasted with the above, sulphate of copper, the basis of most fungicides, requires a $\frac{n}{1}$ concentration to kill the spores of *Penicillium.* Sulphate of zinc was found to have a very low effect on fungi, and so far as *Aspergillus* is concerned, zinc is practically non-toxic, its spores surviving an immersion of forty-eight hours in a $\frac{2n}{1}$ concentration ($=7$ per cent.). Clark expresses surprise at the low toxicity of this salt, considering its extensive use for impregnating railway-sleepers as a preventive against fungi.

Acetic acid is, as a rule, more toxic to fungi than are the mineral acids.

Alcohol in certain proportions appears to enhance vegetative growth and retard fruiting. This was very marked in *Aspergillus* and *Sterigmatocystis* in $\frac{n}{4}$ concentration. *Botrytis* produced greatest abundance of mycelium in $\frac{n}{16}$ and $\frac{n}{32}$. Clark considers that this may be due to alcohol acting as a stimulant rather than as food.

Ono has also shown that very dilute solutions of many mineral salts accelerate vegetative growth, while at the same time retarding or checking the formation of reproductive organs, in *Aspergillus niger*, and *Penicillium glaucum*, also in certain of the lower algae. Under these conditions the energy normally used up in spore-formation is diverted towards the formation of an excess of vegetative hyphae.

Clark, *Bot. Gaz.*, 28, p. 289 and 378 (1899).

Ono, *Journ. Coll. Sci. Imp. Univ. Tokyo*, 13, p. 141 (1900).

INFLUENCE OF FOOD AND ENVIRONMENT ON THE FORMATION OF REPRODUCTIVE ORGANS IN FUNGI

Klebs has investigated the effect of chemical and physical factors on the formation of reproductive organs. In experimenting with *Saprolegnia mixta*, it was found that a total suppression of both sexual and asexual organs occurred when the fungus was supplied with an abundance of nourishment. An abundant formation of zoospores can be secured by starving the fungus, as by growing it in water. On the other hand, if a well-nourished mycelium is placed in a poor medium that is solid, thus precluding the formation of zoospores, sexual organs will be formed in abundance.

In the formation of zoospores the relative value of food depends on the available amount of carbon. Inorganic acids and their salts are of little value. The formation of sporangia is dependent on the presence of potassium phosphate.

As regards temperature the optimum for sexual organs is 26° ; for sporangia, 32°.

The formation of gemmae is of no phylogenetic significance. They are formed under conditions when the formation of other reproductive bodies is rendered impossible, owing to unfavourable environment. On starting growth they behave like ordinary hyphae, and produce sexual organs or sporangia, depending on conditions.

There is no fixed inherent law determining an alternation of generations, but the conditions are such, that under ordinary natural conditions, an alternation is effected, due to the exhaustion of nourishment in each host-plant attacked. Klebs agrees with cytologists generally in considering that morphological characters furnished by an organism at any one period is not sufficient to stamp a species. In future the systematist must determine the limits of variation in a plant, also the causes that determine such variations.

In *Thamnidium elegans*, one of the Mucoraceae, two forms of sporangium are usually present. The terminal one, of large size, is many-spored, with a conspicuous columella and a diffluent sporangial wall. The second form, of which there are usually several, situated laterally on the sporangiophore, is much smaller than the terminal one,

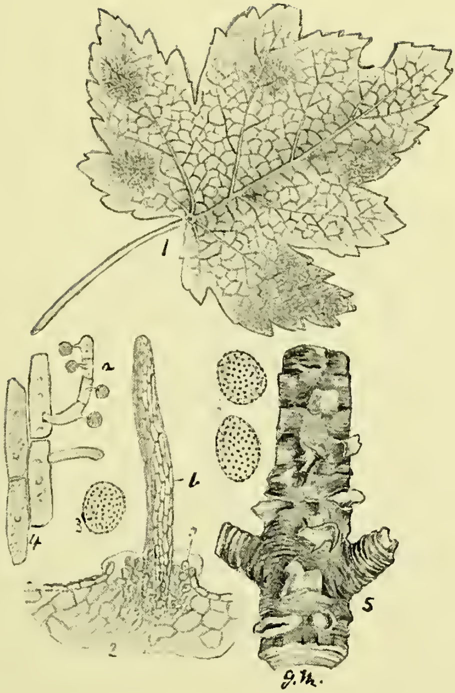

FIG. 41.—*Cronartium ribicolum*, a fungus showing alternation of generations. 1, uredospore and teleutospore stages on leaf of black currant; 2, uredospores, *a*, and teleutospores, *b*, grown together to form an erect, hair-like structure; 3, uredospore; 4, four teleutospores, two of which are germinating: one of the germ-tubes bears four promycelial or secondary spores; 5, aecidial form of fruit on living bark of Weymouth pine: 6, aecidiospores. Figs. 1 and 5, nat. size; the remainder mag.

has no columella, and the sporangial wall is persistent. Bachmann has shown that in this species the various combinations of the two forms of sporangia, or the absence of either, depend entirely on external conditions. Such conditions turn on the chemical composition of food, its degree of concentration, relative degree of humidity, temperature, etc. Any given combination of the two forms of sporangia is constant, so long as the composition of the food and external conditions are also constant.

Varied conditions also affect the external characteristics of spores, and under some instances a totally different form of spore is produced. Biffen says that chlamydospores of *Acrospeira mirabilis*, when grown in air, have a thick, brown, warted wall; when grown in water, the wall is thin, smooth, and uncarbonised.

Klebs's researches throw a new light on laboratory cultures; many of the discrepancies as to results, when dealing with the same kind of fungus, could probably be explained on the ground of differences, chemical and physical, experienced by the different organisms under observation. It is also possible that the general principle enunciated may account for the well-known herding together, in different localities, of male or female plants respectively, in the case of monoecious species.

Bachmann, *Bot. Ztg.*, 1895, p. 107.
Biffen, *Proc. Cambr. Phil. Soc.*, 11, p. 136 (1901).
Klebs, *Pringsh. Jahrb.*, 33, p. 513 (1889).

Ray—a long and interesting account of variation in the lower fungi, due to environment, *Rev. Gen. Bot.*, 9 (1897).

Raciborski—respecting influence of food and surroundings on growth and reproduction of *Basidiobolus ranarum*, *Flora*, 82, p. 107 (1896).

Klebs—gives a general summary of work on physiology of fungi, and additional research, *Pringsh. Jahrb.*, 35, 80 (1900).

FIG. 42.—*Clavaria fastigiata*, a typical saprophyte, growing among grass, and obtaining its food from humus in the soil. Nat. size.

PARASITISM IN FUNGI

From the point of view of nutrition fungi have been arranged under two headings. Saprophytes derive their food from dead or decaying organic matter. Parasites obtain their food from living animals or plants. There are, however, intermediate forms. Some fungi, usually saprophytic, can under certain conditions become true parasites; such are termed facultative parasites. Those fungi which, so far as is known, can only develop and grow on living organisms, are known as obligate parasites. In some instances certain groups of fungi that were considered to be strictly obligate parasites have not proved to be so under all conditions. Brefeld has succeeded in growing several species of *Ustilago* quite independently of the host-

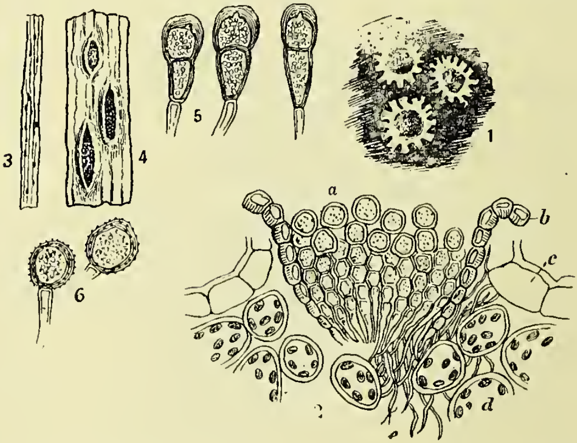

FIG. 43.—*Puccinia pringsheimiana*, a typical obligate parasite. 1, portion of a gooseberry leaf with three aecidia or 'cluster-cups' fully expanded; 2, section through an aecidium, showing, *a*, the spores produced in chains, which afterwards become free and fill the cup with yellow powder, *b*, the protective wall or peridium, *c*, the epidermal cells of the leaf, *d*, the middle cells of the leaf, *e*, the mycelium of the fungus running between the cells of the leaf; 3, portion of the leaf of a sedge, bearing sori or clusters of uredospores and teleutospores; 4, a portion of fig. 3 enlarged; 5, teleutospores; 6, uredospores. Fig. 3, nat. size; all the other figs. mag.

plant. They develop readily on the dung of animals. Certain species were also grown in nutrient solutions.

It has long been known that the parasite gains an entrance into the host by different methods. When the spore or conidium of a parasitic fungus alights on the surface of a leaf that it can infect, germination takes place if conditions are favourable, a certain amount of moisture being usually necessary. In some species the germ-tube produced by the germinating spore always enters through a stoma; in other instances the germ-tube pierces the walls of the epidermal cells, and thus gains an entrance. It has also long been known that a parasitic fungus as a rule can only develop on one particular kind of host-plant, or on a few closely allied plants. The spores and conidia of parasites, carried by wind or other agents, alight on living leaves of all kinds, and readily germinate, but the germ-tube never enters a plant to the extent of developing a mycelium and producing its fruit, unless it happens to be the kind of plant on which the fungus is habitually parasitic. This apparent selection of hosts by fungus parasites I have endeavoured to prove to be due to chemotaxis or chemotropism, which may be defined as the direction of movement due to chemical stimuli. This again means that a germ-tube will only enter the tissue of a living plant, and run its course of development, when there is some special substance or substances present in the cells of the plant which exercise an attractive influence on the germ-tube. Miyoshi, a Japanese botanist, first suggested this idea. He proved that by placing the epidermis of an onion bulb-scale or a thin film of mica through which very minute holes had been pierced, on the surface of gelatine containing a positively chemotactic substance, as dextrin, plum decoction, sugar, etc., the germ-tubes of fungus spores sown on the surface of the epidermis or mica grew towards and finally passed through the stomata or pierced holes into the nutrient substance below. He also demonstrated that the hyphae of *Penicillium glaucum* and species of *Botrytis* passed through the epidermal cells of living leaves, which had previously been charged with a positively chemotactic substance by hypodermic injection.

Certain substances are also known to be negatively chemotactic, and some repellent, either having no directive influence, or deflecting the germ-tubes from their vicinity. A positively chemotactic substance need not necessarily be a food-stuff.

The various chemical substances present in the cells of plants render it difficult in most cases to determine which one or more is chemotactic to a given parasite. I used the cell-sap of the cucumber plant for injection into the living leaf of an orchid still attached to the plant. Spores of a fungus parasitic on cucumber—*Cercospora melonis*—were sown on the surface of the injected portions of the orchid leaf. In due course a few conidiophores bearing conidia appeared on the injected area of the orchid leaf. These spores were in turn sown on other orchid leaves injected with cucumber plant sap. This mode of procedure was repeated twenty-four times, and the spores of the twenty-fourth generation were found to be capable of entering the tissues of the orchid leaf without having to be coaxed inside by injecting cucumber cell-sap. In this case the parasite on cucumber had been gradually educated to accustom itself to the special chemotactic substance present in orchid leaves.

In another experiment, *Trichothecium candidum*, a pure saprophyte so far as at present known, was induced to become a destructive parasite on a species of *Begonia*, by injecting the leaves of the latter with a solution of sugar, to which the germ-tubes of the *Trichothecium* respond strongly. After twelve generations of the fungus produced by the method described for *Cercospora*, the spores of *Trichothecium*, when sown on a living *Begonia* leaf not injected with a solution of sugar, entered the tissues and produced fruit as a parasite. This experiment shows that it is possible to change a saprophyte into a parasite, and also proves that parasitism is an acquired habit on the part of fungi.

In the most severe cases of an epidemic caused by a fungus parasite it is not unusual to observe certain individuals of the same kind as the plants attacked, remaining perfectly healthy, in fact immune against the disease; such immune plants in the case of the cucumber I was enabled to prove to be due to the absence in these plants of the special chemotactic substance that rendered possible the entry of the parasite into the plant. This suggests the line to be taken for the purpose of producing a strain of plants immune against a given parasite.

Sugar in some form is the positive chemotactic substance to which the germ-tubes of nearly all fungi, parasitic and saprophytic, respond, and as this substance is present in the cell-sap of almost every plant in one form or another, the reason why it does not enable any parasite to enter the tissues of any kind of plant is because the positive chemotactic power of sugar is neutralised by the presence of a more powerful repellent substance in the cells.

The results of my observations on the origin of parasitism were summarised as follows:—

1. The entrance of the germ-tubes of a parasitic fungus into the tissues of a living, healthy plant, depends on the presence of some substance in the cells of the host, attractive to the fungus. In other words, infection is due to positive chemotaxis.

2. A saprophytic fungus can be gradually educated to become an active parasite to a given host-plant by means of introducing a substance positively chemotactic to the fungus into the tissues of the host. By similar means a parasitic fungus can be induced to become parasitic on a new host.

3. An immune plant signifies an individual of the same species as the one on which a given species of fungus is parasitic, but which, owing to the absence of the chemotactic substance in its tissues necessary to enable the germ-tubes of the fungus to penetrate, remains unattacked.

Two important papers recently published have, I consider, very materially supported my views respecting the origin of parasitism, as briefly outlined above, although I am not certain that this was the primary intention of either author.

Miss Gibson, acting on a suggestion of Professor Marshall Ward, conducted a series of experiments to see what happened when a plant other than the known host-plant of a given fungus was inoculated. Uredospores and aecidiospores of various species belonging to the Uredinaceae were used for infection, and the hosts were *Ranunculus ficaria*, *Tropaeolum*, *Caltha*, and *Valeriana*. The germ-tubes entered the stomata as in normal infection of the proper host-plant, but within two or at most four days all the hyphae were dead, and in not a single instance was a haustorium formed in the cells of the plant infected. It is pointed out that the evidence is clear that the entrance of the stoma by any germ-tube is no index of the capacity of that germ-tube to infect the leaf. It is very gratifying to note that this is in accordance with my statement on the subject; I made clear that my admitted proof of infection having taken place was the production of fruit by the fungus on the inoculated host-plant. When this did not occur the experiment was put down as a failure. What causes the entry of the germ-tubes was not discovered, but probably a positively chemotropic substance as Miyoshi and others have supposed.

The second paper by Salmon shows that the conidia of certain 'biologic forms' of *Erysiphe graminis* can be induced to infect leaves of host-plants which are normally immune to their attacks after the vitality of the leaf has been affected by cutting out a piece of its tissue, injuring the leaf by touching it with the red-hot point of a knife, cutting away half the thickness of the leaf, treating it with either chloroform, alcohol, etc. In most instances infection followed, and the fungus formed fruit on the injured parts—that is, it grew and fruited on the tissue that has been injured. Salmon's summary of results on this point is as follows:—

'(1) Susceptibility can be induced not only by various kinds of mechanical injury, but also by such interference with the normal function of the cell as follows the application of anaesthetics and heat.

'(2) The conidia of the first generation produced on leaves of a strange host-plant previously subjected to the action of alcohol, ether, or heat, retain the power of infecting their original host, and do not acquire the power of infecting normal leaves of their temporary host.'

These experiments are considered to demonstrate, as they certainly do, the fact that the infective powers of a 'biologic form' are not altered by producing one generation on a mutilated, strange host-plant. Considering that the fungus was grown on mutilated or paralysed portions of the strange host, it was hardly to be expected that its innate affinity for a given host, probably the outcome of an adaptation extending over centuries, should be neutralised or in any way affected. It would be interesting to know what would have happened if the fungus had been cultivated on a mutilated alien host-plant for, say, twenty generations. The experiment, however, came perilously near to demonstrating that what has hitherto been considered as an obligate parasite could live as a saprophyte; if, as suggested above, the experiment had been repeated for twenty times, always using the spores of the previous generation for inoculation, in all probability a saprophyte would have resulted. In other words, the fungus would have been weaned of its predilection for its former host-plant. As the fungus in these experiments was growing on a stratum of cells so treated as to be deprived of the power of exercising the function of either producing or receiving from other cells, those special substances repellent to the fungus when uninjured, it would appear that the fungus responded to some general chemotactic substance, as sugar.

The details of the modes of entry, or infection of a host-plant by a germinating spore, is a somewhat complicated process, and is described by Ward in the case of uredo-spores infecting leaves of *Bromus*, as follows:—

'The germination of the uredo-spore on the epidermis is usually effected during the first twenty-four hours, and the tip of the germ-tube can be seen preparing to enter the stomata in abundance during the second day. I have, moreover, succeeded in fixing, hardening, and staining the germ-tubes and their nuclei, the preparations being then mounted in balsam.

'The young germ-tube grows very rapidly, and the nucleus of the spore soon passes into it, and by suitable methods of hardening and staining can be detected either somewhere along its course or near the tip as it approaches a stoma to enter it. In some cases two or more nuclei are seen in the tube, and the resemblance to a germinating pollen-grain is striking. The first stage in inoculation is evident in the swelling of the tip of the germ-tube over the stoma into a thin vesicle, into which all the nucleated protoplasm derived from the spore passes. This vesicular swelling—the so-called *appressorium*—then puts a thin process down through the stomatal slit, which process again swells into a vesicle on the inner face of the stoma and projecting into the respiratory cavity, and the protoplasmic contents are passed through from the external *appressorium* to the internal vesicle.

'The latter quickly bulges out at one or more points in the form of a tube—the true infecting hypha—into which the whole, or part, of the vesicular protoplasm passes and its nucleus soon divides therein.'

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SYMBIOSIS

After what has been said respecting parasitism it will be seen that every transition between saprophytes and obligate parasites in all probability exists. In every shade of parasitism hitherto discussed the fungus is always dominant to the extent of living entirely at the expense of its host, whereas the latter, so far as is known, receives no benefit from its parasite. In some instances, however, this one-sided condition of things has to a great extent been overcome, and parasite and host respectively benefit. When this point has been reached it is expressed by the term symbiosis or mutualism.

Symbiosis is most evident in Lichens, every member of which consists of a compound body consisting of a fungus and one or more algae. The alga, by virtue of its chlorophyll, forms organic carbon compounds of use to the fungus, whereas the vegetative portion of the fungus supplies the necessary mineral food. Even in this case the fungus appears to be the dominant partner, as it alone is capable of producing fruit, the alga, with very few exceptions, remaining barren.

It has long been known that the rootlets of trees belonging to the Cupuliferae are more or less enveloped in a sheath formed of fungus hyphae. Frank considered this union to be of a symbiotic nature, and we now know that such combinations occur in considerable numbers in every group of vascular and in some cellular plants. In some instances, as in many forest trees, the fungus lives in the humus and forms a compact sheath round the root of its host, which it supplies with a certain amount of water and mineral food-constituents from the soil, and also organic matter derived from humus. In such cases the fungus does not obtain organic food from its host. In other instances the fungal hyphae develop inside the root-cells of the host, which supply them with organic food, and on dying the hyphae furnish albuminoid substances that are absorbed by the host.

Such combinations of fungus hyphae and rootlets have been termed mycorrhiza, are often fleshy and soft, and assume a much-branched coraloid appearance, as in willows, poplars, *Monotropa hypopitys*, etc. Others again cause irregular swellings, as on the roots of alder, and are known as mycodomatia or fungus-chambers. When the hyphae are external as in the Abietineae, the mycorrhiza is said to be ectotropic; when developing in the cells, as in most orchids, endotropic. Root-hairs are not formed on rootlets that have been invested with hyphae.

Mycorrhiza are most abundant when plants are growing in situations where humus is abundant, and may be absent from the same kind of plant in places devoid of humus.

Stahl points out that the rate of transpiration determines to a great extent the presence or absence of mycorrhiza in a plant. Plants that transpire freely obtain their mineral food independent of mycorrhiza, whereas those plants where the transpiration current is slow require the assistance of mycorrhiza to enable them to obtain the requisite supply of mineral food and water. Hence we find growing in the same wood some plants with, and some without, mycorrhiza.

MacDougal and Lloyd have investigated the members of Monotropaceae, a group without chlorophyll, and find the symbiosis between fungus and host to be very perfect, and evidently of ancient origin. As a result the shoots and roots show much degeneration.

In many instances the hyphae of endotropic mycorrhiza, on entering the cell of a host-plant, go direct for the nucleus, which finally becomes surrounded by a coil of hyphae. Groom observed this in *Thismia*, and considered it as due to chemotropism.

In the majority of instances the hyphae forming mycorrhiza have not been connected with any specific fungus. Wahrlich, however, has proved that in certain orchids of the genus *Vanda*, the hyphae belong to species of *Nectria*. *Elaphomyces* forms mycorrhiza on conifers. Members of the Oomycetes, Pyrenomycetes, Gasteromycetes and Basidiomycetes are known to form mycorrhiza.

Trent and Bruchmann consider the fungus found in *Lycopodium* to be a species of *Pythium*, and Rees found the fungus on conifer roots to belong to the genus *Elaphomyces*.

A very remarkable instance of symbiosis has been shown by Freeman to exist between fungus hyphae and *Lolium temulentum*, *L. perenne*, and *L. italicum* respectively. In the first mentioned the yearly life-cycle is completely known; in the remaining two this is not the case as yet, but presumably the departures from that of the known case are not marked. In commercial mixtures of the grains of *L. temulentum*, from eighty-five to ninety-eight per cent. of the total number show a layer of hyphae in the hyaline layer just exterior to the aleurone cells. Along the groove of the grain hyphae are wanting except at the very base where an infection patch occurs, from which hyphae penetrate into the base of the scutellum of the embryo and on to the growing point of the plumule, where a considerable patch of mycelium is formed which remains dormant until germination takes place. On germination the hyphae keep pace in their growth with the growing point, and can be found there throughout the life of the plant. Hyphae are present in all branches and leaf-bases. Their appearance in the latter is considered to be due to similar chemotactic properties in the basal leaf-meristem to those present in the stem growing point. Hyphae develop luxuriantly in the nucellus of the young ovaries, but do not enter the embryo until the latter shows rudiments of the scutellum and growing point, when they pass into the latter, and by the time the grain is mature have formed a patch of mycelium. By these means the mycelium passes from one generation to another by direct infection.

All attempts to induce the fungus to produce spores have resulted in failure, and owing to the certainty of securing infection in a vegetative manner the fungus is apparently able to dispense with the formation of spores.

Owing to the absence of fruit the systematic position of the fungus could not be determined, but the author inclines to the view that its affinities are with the Ustilagineae or 'smuts.'

Infected plants appear to suffer no inconvenience from the presence of the fungus; on the other hand, cultures showed that infected plants were on the average more vigorous, and produced a greater number of seeds than uninfected plants.

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BIOLOGIC FORMS

The phenomenon known as specialisation of parasitism is shown to a remarkable extent in the order *Erysiphaceae*, the Powdery Mildews. This degree of specialisation is due to the evolution—just as in the Rusts (*Uredineae*)—of numerous specialised, or biologic forms, as they are called, within a morphological species. Neger, Marchal, and Salmon have demonstrated by numerous infection-experiments that in the case of a species parasitic on several genera of host-plants the individuals on any one host-species have become specialised in such a way as to be incapable of growing on the other hosts; that is to say, we find on each host-plant a biologic form which is confined either to that one species or to a few closely related species of the same genus. Thus the morphological species *Erysiphe graminis*, DC., is found on barley, oat, wheat, rye, and a number of wild grasses belonging to various genera (*Bromus*, *Poa*, *Dactylis*, *Agropyrum*, etc.). Experiments have proved, however, that on each of these host-plants the fungus has become specialised, with the result that the form on barley cannot infect oat, wheat, rye, etc.—that on wheat cannot infect barley, oat, rye, etc.—and so on. These biologic forms are morphologically indistinguishable from one another, but differ physiologically or biologically in possessing distinctive and sharply defined infection-powers.

Further, it has been found that this phenomenon, which was first observed in the conidial (*Oidum*) stage of the fungus, occurs also in the ascigerous stage. In experiments carried out by Salmon, ascospores of individuals of *E. graminis* grown on barley were sown on barley, *Hordeum Zeocriton* and *H. trifurcatum* (two closely allied species), and on *H. maritimum*, *H. secalinum*, *H. jubatum*, *H. bulbosum*, oat, wheat, and rye. Infection resulted only on barley, and on the two species closely allied to it, *H.*

Zeocriton and *H. trifurcatum*; all the other host-plants proved persistently immune, although they are capable of being readily infected by other biologic forms of *E. graminis*. Marchal, in similar experiments, has proved that ascospores taken from the form of *E. graminis* on wheat can infect wheat, but not rye, barley, or oat.

So far as experiments have been carried out, it appears that the infection-powers of the ascospores of biologic forms are identical with those of the conidia; thus the specialisation of parasitism is as sharply marked and as distinctive in the ascigerous as in the conidial stage. Since, then, biologic forms show restriction in their power of infection to one species of host-plant, or to a few closely allied species, in the sexual ascigerous stage as well as in the asexual conidial stage, we must admit their claim to be considered as distinct entities.

The extent to which this specialisation has proceeded in some cases is shown in a recent paper by Salmon on the adaptive parasitism of *E. graminis* to species of the genus *Bromus*. The author, as the result of nearly two thousand inoculation experiments, ascertained the presence of a considerable number of well-defined biologic forms, each possessing distinctive powers of infection towards certain species of *Bromus*. The characteristics of four of these biologic forms are represented in the following schedule :—

Oidum on	Sown on								
	B. mollis.	*B. interruptus*	*B. commutatus*	*B. secalinus*	*B. velutinus*	*B. racemosus*	*B. arvensis*	*B. tectorum*	*B. sterilis*
B. interruptus	+(48)	+(10)	– (42)	–(25)	+ ?(10) – (15)	–(11)	–(29)	+ (16)	–(20)
B. hordeaceus	+(29)	+(34)	+ (40) – (9)	+? (9) – (13)	+ ?(10) – (6)	–(15)	–(28)	+ (21)	–(13)
B. commutatus	–(13)	– (9)	+(117) – (1)	+(22) – (3)	+ (6) – (1)	–(43)	–(10)	+ ?(16) – (13)	– (7)
B. racemosus			– (12)			+(27)		– (3)	

The sign + indicates full infection; the sign – denotes that no infection followed inoculation; the sign +? is used when only 'subinfection' resulted. The number of leaves of each species inoculated is shown within brackets.

The biologic form on *B. interruptus* is characterised by producing full infection when sown on *B. mollis*, *B. interruptus*, and *B. tectorum*; it produces either slight infection on *B. velutinus*, or passes over this species; and causes no infection on *B. commutatus*, *B. secalinus*, *B. racemosus*, *B. arvensis*, and *B. sterilis*. The biologic form on *B. hordeaceus* is distinct in nearly always infecting *B. commutatus*, and in sometimes causing slight infection on *B. secalinus*. The biologic form on *B. commutatus* differs in being unable to touch *B. mollis* and *B. interruptus*. The biologic form on *B. racemosus* differs from all the others in infecting *B. racemosus*.

The facts obtained show not only the high degree of specialisation reached by the fungus in its adaptive parasitism to the various species of the genus *Bromus*, but demonstrate also that each species of *Bromus* possesses distinctive physiological (or constitutional) characters existing concomitantly with the specific morphological characters. By using the index of the reaction to the attacks of the biologic forms of the fungus, it can be demonstrated that species of plants very closely allied systematically may possess different physiological characters. Thus the two plants *B. commutatus* and *B. racemosus*—which are so close morphologically that the majority of systematists hold that *B. racemosus* is nothing more than a variety of *B. commutatus*—are proved to differ physiologically by the fact that the fungus on *B. commutatus* cannot infect *B. racemosus*, and *vice versâ*.

Now, although as a rule each species of *Bromus* shows physiological characters which hold good for all examples of the species derived from different localities, there are exceptions to this rule, and we find that the inter-relations between the biologic forms of the fungus and certain of their host-plants become complicated by the existence of biologic forms of the host-plant. Such a case is illustrated diagrammatically at fig. 44. Here we have shown the results of experiments in which *B. mollis* and a plant called *B.* '*hordeaceus*' were inoculated with conidia of the forms of

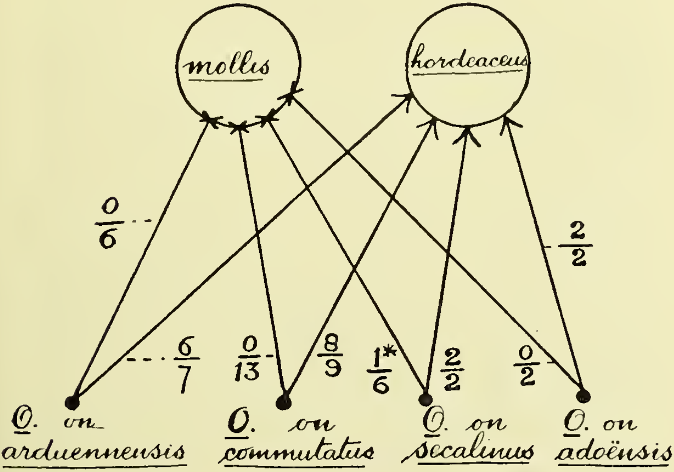

FIG. 44.—In this diagram, and in the following one, the number of inoculations made and the results obtained are expressed in the form of a fraction, in which the numerator indicates the number of times in which infection resulted, and the denominator the number of leaves inoculated.

the fungus growing on *B. arduennensis*, *B. commutatus*, *B. secalinus*, and *B. adoënsis*. In every case *B.* '*hordeaceus*' proved susceptible, while *B. mollis* remained immune. Nevertheless, *B.* '*hordeaceus*' proved on close examination to be identical morphologically with *B. mollis*. These results lead us to conclude that the morphological species *B. mollis* includes two 'races' or sets of individuals possessing distinctive physiological (or constitutional) characters, that is to say, an immune and a susceptible race with regard to the form of the fungus in question. These may be termed biologic forms of a host-plant.

Another interesting fact is the discovery of certain host-plants which function as 'bridging species.' It has been found that a number of biologic forms may all be able to infect a certain host-plant, although each one of these biologic forms may be incapable of infecting the host-plants on which the others occur.

Thus fig. 45 represents diagrammatically the results of certain infection-experiments, from which we see that the biologic forms of the fungus on *B. secalinus*, *B. interruptus*, *B. racemosus*, *B. commutatus*, and *B. arduennensis* are all able to infect *B. hordeaceus*, although they are incapable of the reciprocal infection of their host-plants. With the existence of such inter-relations as these the question at once presented itself whether *B. hordeaceus* might not act as a 'bridge,' affording a passage for certain biologic forms to species of host-plants which they are unable to attack directly. Actual experiments have proved this to be the case. It has been ascertained by repeated inoculation-experiments that the biologic form on *B. racemosus* is unable to cause any infection whatever on *B. commutatus*; infection by means of a 'bridging species' (of host) has, however, been found to take place. In certain experiments conidia were taken from *B. racemosus* and sown on *B. hordeaceus*. Infection resulted at once, a crop of conidia being produced on *B. hordeaceus* in a few days. These conidia were now sown on *B. commutatus*, and proved capable of infecting this species. That is to say, *B. hordeaceus* here acted as a 'bridge,' enabling the fungus on *B. racemosus* to pass over to *B. commutatus*, a species which is safe against its direct attack.

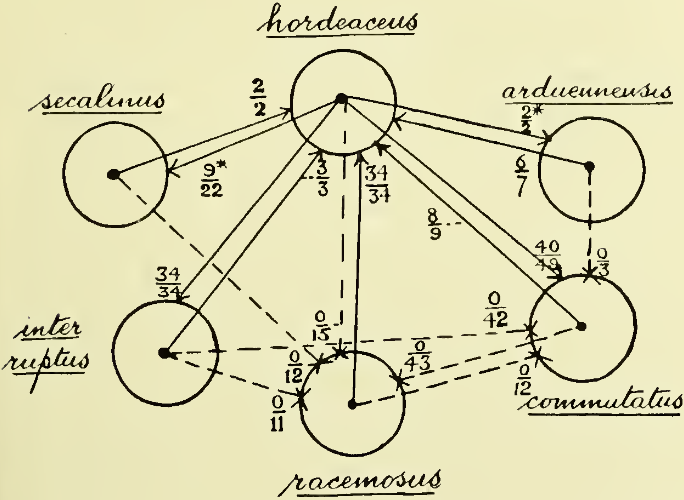

FIG. 45.

Thus we see that in certain cases the infection-powers of a biologic form may be considerably influenced by the effect of its residence on a new host-plant.

This leads us to the interesting question whether the immunity shown by certain host-plants to certain biologic forms is permanent under various conditions, a subject lately investigated by Salmon, in a series of experiments which gave the following results. The host-plant chosen was barley, the fungus being the biologic form of *E. graminis* on wheat. It had previously been ascertained by repeated experiments that this biologic form on wheat is not able, under ordinary conditions, to infect barley. In these experiments plants of barley were abundantly inoculated with both conidia and ascospores, while others were allowed to stand for several months among virulently infected wheat plants, where they were constantly exposed to infection; in every case the barley plants remained persistently immune. By using certain cultural methods, however, Salmon succeeded in rendering barley susceptible to infection by the biologic form on wheat. The barley before being inoculated was treated as follows: The leaves were either (1) mechanically injured locally in one of the following ways—a small portion of leaf-tissue was cut out, or pressure was applied so as to bruise a group of leaf-cells, or the surface of the leaf was touched at one spot with the red-hot point of a knife, or the leaf was injured by allowing slugs to eat out large pieces; or (2) the whole leaf was exposed for a short time to the action of ether or chloroform, or immersed in a mixture of alcohol and water, or heated up to 50° C. in water. The treated barley leaves were then inoculated with ascospores or conidia taken from the biologic form on wheat, and proved susceptible. In the case of the mechanically injured leaves only the cells immediately adjoining the place of injury became infected; in the cases where an anaesthetic or heat was employed, infection resulted here and there over the whole surface of the leaf. In both cases patches of mycelium producing conidia were obtained on the barley leaves.

We may mention here the hypothesis, advanced by Salmon, as to the factors determining infection, and the explanation given of the susceptibility shown by injured leaves to the attacks of biologic forms which are unable to infect normal leaves of the species in question. It seems clear from the result obtained in the following experiment that the immunity or susceptibility of a given species in no way depends on any structural or anatomical peculiarity of its leaves (nature of the cell-wall, the presence of hairs, ribs, etc.). If a leaf which has proved persistently immune to the attacks of a certain biologic form is cut with a razor in such a way that the epidermal cells on one surface, and all or most of the mesophyll tissue are removed at the cut place, but the epidermal cells on the other surface (opposite the cut) are left uninjured, and then conidia or ascospores of the same biologic form are sown on the cuticular surface of the uninjured epidermal cells over the wound, infection will now result. It is necessary to assume, therefore, that the physiological characters possessed by the leaf-cells are the determining causes governing infection and immunity.

On general grounds we may assume the existence of enzymes, or toxins, in the cells of the fungus, and of antitoxins or similar substances in the cells of the host-plant. We may suppose further that the leaf-cells of the various host-species—wheat, barley, etc.—contain, or are able to produce, substances peculiar to each species, which, when the leaf is uninjured and the cells are vigorous, are able to prevent the successful attack of any mildew except the one biologic form which has become specialised to overcome the resistance. Now, in the cases described above, in which species of plants were rendered susceptible to biologic forms which are incapable under ordinary conditions of infecting them, the cultural methods adopted consisted in affecting the vitality of the leaf either by a mechanical injury or by the action of anaesthetics or heat. When the vitality[1] of the cell becomes affected through the injury to the leaf, it may be assumed that either the protective enzymes or similar substances normally present are destroyed, or become weakened, or the production of them by the protoplasm is interfered with, in the cells in the neighbourhood of the injury, with the result that other biologic forms are now able to cause infection, since they no longer meet with any special substance capable of stopping their growth. It is pointed out that these cases of the loss of immunity, brought about by causes which affect the vitality of the leaf, find their exact parallel in the recorded instances of induced susceptibility in animals to certain bacterial diseases. The decrease of vitality caused by fatigue, action of drugs, abnormal food, or environment, has been proved to induce susceptibility to certain bacteria in the case of an animal which had proved to be immune under normal circumstances.

Salmon suggests that in nature injuries to leaves, having the same effect as those caused artificially in the experiments mentioned above, may be caused by animals, hail, storms of wind, etc., and mentions cases where, apparently,

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[1] The author remarks: 'Until our knowledge of the physiology of the cell has progressed further, it is necessary to use the general term vitality to express the sum of the individual physiological processes at work in the cell. External factors which affect the normal balance in the working of the individual physiological processes may be said to increase or decrease the vitality of the plant.'

susceptibility was induced through the injury to a leaf caused by the attacks of the 'green fly' (*Aphis*).

Neger, F. W., 'Beiträge zur Biologie der Erysipheen,' *Flora*, 90, p. 221 (1902).

Marchal, E., 'De la spécialisation du parasitisme chez *l'Erysiphe Graminis*,' *Comptes Rendus*, 135, p. 210 (1902); 136, p. 1280 (1903).

Salmon, E. S., 'On Specialisation of Parasitism in the *Erysiphaceae*,' *Beihefte z. Botan. Centralbl.*, 14, p. 261 (1903); *idem*, ii., *The New Phytologist*, 3, p. 109 (1904); *idem*, iii., *Annal. Mycolog.*, 3, p. 172 (1905).

Salmon, E. S., 'Infection-powers of Ascospores in *Erysiphaceae*,' *Journ. of Bot.*, 41, p. 159 (1903).

Salmon, E. S., 'Cultural Experiments with the Barley Mildew, *Erysiphe graminis*, DC.,' *Annal. Mycolog.*, 2, p. 70 (1904).

Salmon, E. S., 'On *E. graminis*, DC., and its adaptive parasitism within the genus *Bromus*,' *l.c.*, p. 255 (1904).

Salmon, E. S., 'Cultural Experiments with an *Oidium* on *Euonymus japonicus*, Linn. f.', *l.c.*, 3, p. 1 (1905).

Salmon, E. S., 'Cultural Experiments with "Biologic Forms" of the *Erysiphaceae*,' *Phil. Trans.*, 197, p. 107 (1904).

Salmon, E. S., 'Further Cultural Experiments, etc.', *Annals of Bot.*, 19, p. 125 (1905).

HETEROECISM IN FUNGI

The majority of parasitic fungi go through the entire course of their development on a single host-plant; such are termed autoecious. On the other hand, a considerable number of species belonging to the Uredinaceae grow on a different kind of host-plant during the different periods of their complete cycle of development; such are said to be heteroecious, or metoecious as preferred by De Bary, who first clearly described this phenomenon as presented by *Puccinia graminis*. The teleutospores or resting-spores of this fungus pass the winter on the dead culms of various wild or cultivated kinds of grass. During the following spring the teleutospores germinate *in situ*, producing minute secondary spores that are dispersed by wind. These secondary spores will not directly infect a grass plant, but those that happen to be deposited on the surface of a young barberry (*Berberis vulgaris*) leaf, germinate at once, the germ-tube enters the tissues of the leaf and soon gives origin to groups of aecidia or 'cluster-cups' crowded with golden-yellow aecidiospores. Structures called spermogonia also develop on the barberry leaf along with the aecidia, and are supposed to represent male organs that have persisted from a period when they were considered to have been of functional value.

The aecidiospores will not directly infect a barberry plant, but when placed on the leaf of a suitable grass, infection takes place, and in due course pustules of uredospores appear on the surface of the grass leaf. Uredospores, on the other hand, will only infect grasses, and the production of uredospores and infection of new grasses continues throughout the summer. During the autumn, when the host-plant is on the wane, the mycelium, that up to the present had been producing uredospores, now commences to produce teleutospores, in fact during the transition period it is not unusual to find both uredospores and teleutospores present in the same pustule. At a later

FIG. 46.—*Puccinia graminis,* an heteroecious fungus producing different kinds of spores on different hosts, and on the same host at different periods. 1, leaves of wheat plant with pustules of uredospores; 2, a pustule or group of uredospores more highly mag.; 3, uredospores in various stages of development; 4, uredospores germinating; 5, portion of a wheat stem showing pustules of teleutospores; 6, teleutospores in various stages of development; 7, teleutospores germinating; 8, a barberry leaf bearing groups of the aecidium or 'cluster-cup' form of fruit; 9, section of an aecidium containing spores in chains; 10, two aecidia seen from above; 11, sporules from a spermogonium. Figs 1, 5, and 8, nat. size; remainder mag.

period, however, teleutospores are alone present. The production of teleutospores completes the cycle of development of the fungus. The following spring the teleutospores germinate, infection of the barberry follows, and the cycle of development commences anew.

Puccinia graminis is a very injurious parasite to cereals, and at one time it was thought that if the cycle of development could be broken by removing one of its host-plants —the barberry—the disease would be arrested. This line of reasoning unfortunately has not proved to be correct. The fungus is capable of going on as usual when the aecidium stage has been eliminated from its cycle of development. This fact does not support the view recently announced that the aecidium condition gives a stimulus to the general development of the fungus. In some species of the Uredineae the teleutospore stage alone is present, as in the hollyhock rust (*Puccinia malvaccarum*). The aecidial stage has dropped out in many species.

De Bary, *Neue Unters. ü. Uredineen*, *Monatsbr. d. Berlin Akad.*, Jan. 1865 and Apr. 1866.

MYCOPLASM

Eriksson has arrived at the conclusion that the sudden and widespread epidemics caused by the rust fungus of wheat are not entirely due to external infection of the host by spores dispersed by wind and other agents. The theory is advanced that in certain varieties of wheat, more especially the form known as 'Horsford pearl,' the protoplasm of the rust fungus is present, mixed with the protoplasm of the host, in the 'seed.' To this mixture of protoplasm of parasite and host Eriksson has applied the name of mycoplasm. When such infected seed is sown the fungus protoplasm remains unchanged until the plant has produced leaves, when it materialises, or separates from the protoplasm of the host, and forms structures termed 'special corpuscles' in certain cells of the host-plant, at those points where uredo-pustules will eventually appear. These special corpuscles are described by Eriksson as occurring mixed with the other elements of the cells, most frequently oblong in form, sometimes slightly curved. Some of these bodies lie free in the protoplasm of the cell, others are attached to the cell-wall of the host, which they pierce and form outside an intercellular mycelium. This intercellular mycelium eventually gives origin to a sorus of uredospores.

This remarkable theory has been thoroughly investigated by Ward, who has shown that Eriksson's special corpuscles, considered as the first products of materialisation from mycoplasm, are in reality nothing more than ordinary haustoria that have entered certain cells from intercellular mycelium, itself the product of external infection caused by germinating uredospores. Hence the mycoplasm theory appears to be altogether unsupported by facts, although it must be stated that the idea is not yet abandoned by its originator.

Eriksson, *Compt. Rend.*, 124, p. 475 (1897).
,, *Ann. Soc. Nat.*, ser. 8, 15, p. 193 (1902).
Ward, *Phil. Trans. Roy. Soc.*, 196, p. 29 (1904).

CHEMISTRY OF FUNGI

SUGARS

Mannite, trehalose, and glucose have been found in many kinds of fungi by Bourquelot; of these the two first named are crystallisable. Mannite occurs most generally; glucose is often present in young specimens, becoming partly transformed into mannite as the fungus matures.

The following genera are characterised by the presence of trehalose: *Cortinarius*, *Coprinus*, *Hypholoma*, *Hebeloma*, and *Pholiota*. Mannite alone is present in *Russula*, *Lactarius*, *Psalliota*, *Lepiota*, and *Peziza*. The relative distribution of sugars is constant and characteristic of certain genera.

Bourquelot gives the proportion of saccharine matters present in one kilogram of fresh tissue, from various parts of *Boletus edulis*. Stem, 24·5 grams of trehalose, and 0·77 gram of glucose. Pileus, 13·8 grams of trehalose, 0·71 gram glucose. Saccharine matters are absent from the tubes. This distribution of sugars is considered to explain why the larvae of Diptera are confined in their attacks to certain portions of a fungus.

FATS AND OILS

These bodies are often present as reserve substances, in many reproductive bodies, as oospores and zoospores of Chytridiaceae and Saprolegniaceae, uredospores, basidiospores, ascospores, etc. Large quantities are also often present in the mycelium, that of *Lactarius deliciosus* containing about six per cent. Sclerotia also, as a rule, contain large quantities, that of *Claviceps purpurea* containing, according to Zopf, thirty-five per cent.

Cholesterine

The cholesterines present in fungi are unstable when exposed to air. Gérard has detected their presence in *Lactarius piperatus*, *L. vellereus*, *Penicillium glaucum*, and also in the Myxogaster, *Aethalium septicum.*

Tannin

Naumann states that tannin is most abundant in the Polyporeae, occurring only very sparingly in Agarics. It is also more abundant in parasites than in saprophytes.

Ergotinine

This substance, discovered by Tauret, is the only definite chemical compound of therapeutical value present in ergot, the other bodies known as ergotine (Wenzell), picrosclerotine (Dragendorff), etc., being mechanical mixtures. It crystallises as fine, colourless, microscopic needles which colour quickly when exposed to light. Fusion point about 205°. Insoluble in water, quickly soluble in chloroform.

Muscarine

Found by Schmiedelberg and Koppe in *Agaricus muscarius*; it is also said to be the poisonous principle in *Boletus luridus* and *Agaricus pantherinus.* It is a crystallisable, very deliquescent alkali, soluble in alcohol. Treated with potash it decomposes, and gives off trimethylamine.

It is very poisonous. A dose of 0·003 gram to 0·005 gram is sufficient to cause serious symptoms in a human being. Atropine is considered as an antidote.

PHALLINE

A poisonous principle present in *Agaricus phalloides*. Kobert states that this substance causes dissolution of the red corpuscles of the blood to a remarkable extent. This action is evident when the poison is diluted to one part in 125,000.

CARBON BISULPHIDE

Went says that *Schizophyllum lobatum*, found chiefly on dead stems of bamboo, and of sugar-cane, forms carbon bisulphide.

Bourquelot, *Bull. Soc. Myc. France*, 5, p. 341 (1889), and in every succeeding volume to 9 inclusive.

Bourquelot, *Compt. Rend.*, 113, p. 749 (1891).

Gérard, *Bull. Soc. Bot.*, 1890, p. 115, and 1892, p. 169.

Kobert, *Lehrb. d. Intoxikationen*, p. 457.

Nordmann, *Ueber den Gerbstoff der Pilze*; Inaug. Dissert., Erlangen, 1895.

Schmiedelberg and Koppe, *Vierteljahrsch. f. Pharm.*, 19, p. 276 (1870).

Tauret, *Compt. Rend.*, 1875, p. 896, and 1878, p. 888.

Went, *Ber. d. deutsch. Bot. Ges.*, 14, p. 158 (1896).

Zopf, *Die Pilze*, p. 138.

Husemann and Hilger, *Die Pflanzenstoffe*, Berlin, 1882. 2 vols. Contains a full account of the numerous substances found in fungi.

COLOURS OF FUNGI

Respecting the origin or uses of colours in fungi, but little is known with certainty. Clear bright colours are present in some of the larger Pezizae, *Peziza aurantia*, *P. coccinea*, etc., but it is in the Basidiomycetes that we encounter the greatest variety of brilliant tints. Red passing through orange to yellow are the predominating colours, and many of these are stated by Zopf to belong to the group of carotins. From the perithecia of *Bulgaria inquinans* this author isolated and extracted six substances: (1) A red substance, soluble in water, called bulgarerythrine; (2) A second red body, insoluble in water, bulgarüne; (3) A blue substance, insoluble in water, bulgarocoerulene; (4) A resinous acid, ranging from reddish-yellow to reddish-brown, bulgaric acid; (5) An amorphous yellow body, soluble in water, in very small quantity, and could not be chemically examined; (6) A yellow oil.

Certain colours or shades are often characteristic of genera, or sections of genera. In one group of *Hygrophorus* all the species are brilliantly coloured, ranging from deep crimson to canary-yellow in different species. Blue is the predominating colour in the genus *Leptonia*. In *L. chalybea* every part is deep ultramarine, in other species the blue is not so pure, whereas in several species the stem alone retains the blue colour. It is a significant fact, probably indicative of a common origin, that in several groups of allied species, there is a common bond indicated by the predominance of some one colour present in the stem. As an instance, the blue or greenish-blue colour of the base of the stem in several species of *Inocybe* may be noted.

In the Gasteromycetes bright colours are almost entirely confined to the Phalloideae, where the hymenium is very frequently red. The supposed function here is attractive, in connection with spore dissemination.

FIG. 47.—*Calocera viscosa*, a gelatinous fungus of a clear orange colour, common on dead stumps of conifers. Nat. size. (Photo by Saville-Kent.)

Spores are very frequently coloured, the most pronounced instance occurring in *Ascobolus*, a genus of Discomycetes, growing mostly on dung. The spores, at first colourless, change through pale lilac to clear deep amethyst. In *Sporormia*, a genus belonging to the Sphaeriaceae, and also growing on dung, the spores are first colourless, then clear green, afterwards purple, and finally opaque brown.

In the great majority of instances the colouring matter of spores is confined to the wall, and in some instances to the outer layer of this structure, as in the examples mentioned above. In some cases the contents of the spore are alone coloured, the wall remaining colourless, as in many aecidiospores, the spores of *Bactridium*, etc.

In hyphae that are coloured the colour is also generally confined to the cell-wall, although Biffen states that in some hyphae the colour is located in the contents, the wall remaining hyaline.

The flesh of many species of *Boletus* changes from white or yellow to a deep indigo-blue when broken and exposed to the air. Schönbein first showed that the flesh of *Boletus luridus* possessed the property of turning an alcoholic solution of guiacum blue. This was explained on the assumption that the fungus possessed the property of converting the oxygen of the air into ozone, and that the ozone reacted on the guiacum, producing a blue coloration.

Bourquelot and Bertrand have recently investigated this point, and have observed that a similar property is possessed by numerous fungi belonging to various groups. They have verified Schönbein's observation given above, and consider the action due to the presence of an oxidising ferment present in the fungus. This ferment they call tyrosinase. It is further stated that those fungi whose broken flesh becomes coloured in contact with air contain chromogenous materials. That is to say, they contain substances which, when oxidised, are transformed into coloured products, and that the colours of such species as *Lactarius deliciosus*, *Russula lepida*, and *Clitocybe inversa* are due to the oxidation of bodies which form a pigment in the hyphae of the cuticle of the fungus. This explanation receives support from the fact well known to all those who are familiar with fungi in their native haunts, that in cases where the pileus is normally coloured, those portions of its surface protected from the action of the air by the adhesion of a leaf remain colourless.

The brilliant vermilion colouring matter of the Fly Agaric, *Amanita muscaria*, has been investigated by Griffiths, who calls it amanitin. It is insoluble in water, soluble in chloroform and ether. Solutions give no characteristic absorption bands in the spectroscope.

The intense verdigris-green colour of *Helotium aeruginosum* and allied species has been the subject of much speculation. The subject has recently been investigated by Vuillemin, who shows that the green colouring matter is a product of the fungus and not an obligate parasitic Bacterium, as has been suggested. It is located in masses in the lumen of the hyphae, and not in the wall, and is considered as a reserve substance. Liebermann has obtained the green substance as pure crystals, and calls it Xylindein.

Finally, Prillieux states that Xylindein in a solution of chloroform shows under a spectrum analysis certain rays of absorption parallel with those of chlorophyll, but that it does not act under the influence of light as chlorophyll does.

Nadson, a Russian chemist, has made some interesting observations on the nature and origin of the colouring matters of fungi.

Bourquelot and Bertrand, *Bull. Soc. Myc.*, 1896, p. 17.

Griffiths, *Compt. Rend.*, 1896, p. 1342.

Liebermann, *Ber. d. deut. Chem. Ges.*, Bd. 7, p. 1102 (1874).

Nadson, *Trav. de la Soc. Nat. de St. Petersb.*, 1891.

Prillieux, *Bull. Soc. Bot. France*, 2, May 1877.

Vuillemin, *Bull. Soc. des Sci. de Nancy*, 1898.

Zopf, *Beitr. zur Morph. und Physiol. niederer Org.*, 1892.

CHEMOTAXIS (=Chemotropism)

The direction of movement influenced by chemical stimuli. This term was suggested by Pfeffer, who, in experimenting with the antherozoids of cryptogams, protozoa and bacteria, showed that not only food-stuffs, but also solutions of various salts, acids, and alkalies possessed the power of directing the movements of these organisms. Certain of these substances exercise an attractive influence —positive chemotaxis; others exercise a repelling influence—negative chemotaxis. Following Pfeffer, Miyoshi cultivated fungi in gelatine containing a small amount of sugar, which was separated by a membrane from a second layer of gelatine containing a larger proportion of sugar; the hyphae bored through the membrane into the layer containing the largest amount of sugar. He also showed that the hyphae of *Penicillium glaucum* and species of *Botrytis* passed through the epidermal cell-walls of living leaves, which had previously been injected with a positively chemotactic substance. The germ-tubes of *Penicillium* *glaucum* bored through the cell-walls of elder pith, and passed through the pits of coniferous wood that had been injected with a positively chemotactic solution.

Chemotropism is supposed to be the directive force accounting for many phenomena presented by fungi. Lind considers that the penetration of fungi into chalk, egg-shell, or bone is due to a chemotactic stimulus furnished by an organic or inorganic food-material. Groom states that the hyphae of a mycorrhiza present in *Thismia*, on entering a cell, go directly to the nucleus owing to this same influence. I have shown that a specific substance or substances present in the cells of a plant is the prime factor in attracting the germ-tubes of parasitic fungi into the tissues of the host-plant. Only the germ-tubes of the fungus that responds to such attraction can enter the plant; consequently, when a spore germinates on other than the host having the chemotactic substance to which the germ-tube responds, no infection takes place. This accounts for the same kind of fungus being always parasitic on the same kind of host-plant, or on allied species.

Groom, *Ann. Bot.*, 9, p. 327.
Lind, *Pringsh. Jahrb.*, 32, p. 603 (1898).
Massee, *Phil. Trans. Roy. Soc.*, ser. B., 197, p. 7 (1904).
Miyoshi, *Bot. Ztg.*, 1894, p. 1.
,, *Pringsh. Jahrb.*, 28, p. 269 (1895).
Pfeffer, *Ber. d. deutsch. Bot. Ges.*, 1, p. 524 (1883).

CHEMAUXISM

This term is used by Renard to express the acceleration of growth due to the presence of salts of copper in definite proportions, acting in conjunction with certain nutrient substances.

Among the hydro-carbons, glucose enables copper salts to exercise their peculiar property to the greatest extent. Germination is not affected by salts of copper. *Penicillium glaucum* was the fungus used for the experiments.

Renard, *Journ. de Bot.*, 1902, p. 97.

BECQUEREL'S RAYS (=Radium rays)

Dauphin has experimented with these rays on *Mortierella*, and finds that they arrest the growth of the mycelium, and prevent the germination of spores. These are not killed but simply paralysed or rendered latent, and germinate or continue growth when placed under normal conditions. Cysts are formed in the interior of the cells of the mycelium, which are obviously protective bodies produced under the exceptional conditions.

Dauphin, *Compt. Rend.*, 138, p. 154 (1904).

ROENTGEN RAYS

Koernicke finds that these rays inhibit the growth of fungi after prolonged action.

Koernicke, *Ber. d. deutsch. Bot. Ges.*, 1904, pp. 22 and 148.

LUMINOSITY OF FUNGI

The fact that certain fungi emit a more or less brilliant phosphorescent glow has long been known. The phenomenon is most frequently connected with Agarics, and more especially species of *Pleurotus*, and has been recorded from Brazil, Borneo, India, Java, Australia, etc. The olive-tree agaric, *Pleurotus olearius*, is the most conspicuous example in Europe of a luminous fungus. *Corticium coeruleum*, *Armillaria mellea*, and the ascigerous species, *Xylaria hypoxylon*, and *X. polymorpha*, are also said to be luminous. Sterile mycelium in decayed wood, rhizomorphs, and sclerotia also possess the same property. The following account by Berkeley will give some idea of the phenomenon. A quantity of wood had been purchased in a neighbouring parish, which was dragged up a very steep hill to its destination. Amongst it was a log of larch or spruce, it is not quite certain which, twenty-four feet long and a foot in diameter. Some young friends happened to pass up the hill at night and were surprised to find the road scattered with luminous patches, which, when more closely examined, proved to be portions of bark or little fragments of wood. Following the track, they came to a blaze of white light which was perfectly surprising. On examination, it appeared that the whole of the inside of the bark of the log was covered with a white byssoid mycelium of a peculiarly strong smell, but unfortunately in such a state that the perfect form could not be ascertained. This was luminous, but the light was by no means so bright as in those parts of the wood where the spawn had penetrated more deeply, and where it was so intense that the roughest treatment scarcely seemed to check it. If any attempt was made to rub off the luminous matter it only shone the more brightly, and when wrapped up in five folds of paper the light penetrated through all the folds on either side as brightly as if the specimen was exposed. When, again, the specimens were placed in the pocket, the pocket when opened was a mass of light. The luminosity had now been going on for three days.

Phosphorescent mycelium and fungi are not uncommon on woodwork in mines.

Gardner describes how, in a town in Brazil during one dark night, he observed some boys amusing themselves with some luminous objects, which he supposed to be a kind of large fire-fly, but which on examination proved to be a beautifully phosphorescent Agaric, which he was told grew abundantly in the neighbourhood on the decaying fronds of a palm. The whole plant gives out at night a bright light, having a pale-greenish hue.

A satisfactory explanation as to the causes promoting luminosity is not as yet forthcoming. It is considered by Fabre as an expression of the respiration of the cells. In all phosphorescent species of Agarics the phenomenon is most pronounced in those portions where growth is most vigorous, as the margin of the pileus, gills, apex of stem, etc., whereas mature spores are not phosphorescent. The emission of light depends on a specific property of the protoplasm, and is not simply due to oxidation.

Berkeley, *Gard. Chron.*, 1872, p. 1258.

Gardner, in *Hook, Journ. Bot.*, 2, p. 426 (1840).

Fabre, *Compt. Rend.*, 41, p. 1245, and in *Flora*, 1856, p. 220.

Phillips, *Luminosity of Fungi*, records of Woolhope Club, 1881.

GEOGRAPHICAL DISTRIBUTION OF FUNGI

Our knowledge respecting the fungus flora of tropical countries is as yet too imperfect to admit of any detailed, or even approximate, account of the distribution of the various groups of fungi being attempted. Although evidence is not lacking as to the existence of Agarics and other fleshy fungi in tropical forests, the difficulty in preserving such in a condition to be afterwards recognised, even generically, is so great that it is but rarely attempted. On the other hand, the dry, woody, or corky substance characteristic of tropical species belonging more especially to Polyporaceae and Thelephoraceae renders their collection and preservation so easily accomplished, that such have been spoken of as specially characteristic of tropical regions. This, however, is not a fact, as in those few instances where persons resident in the tropics have made mycology a special study, the result has been to show that representatives of all known families are present. As instances of such careful work done in tropical and subtropical countries, may be instanced the extensive collections, accompanied by coloured figures and full notes, made by Thwaites in Ceylon, and described by Berkeley and Broome, by Wright in Cuba, and by Möller in South America.

Fungi, being either parasitic or saprophytic on the higher plants, consequently follow closely in the wake of the latter; and perhaps, speaking broadly, it may be stated that fungi are most aggressive and numerous where their hosts are placed under a disadvantage. Instances of this kind are too well known in the instance of most cultivated plants, which as a rule suffer more severely than uncultivated plants of the same kind. One reason for this is that cultivated plants are usually introduced species and far removed from normal conditions by the excessive development of one special part, at the expense of the others. I have been much interested, during the examination of collections of plants from Arctic regions, to observe the comparatively large number of parasitic fungi present, mostly belonging to the Sphaeriaceae and Sphaeropsideae; again indicating that under conditions presumably not ideal for phanerogamic development the simpler fungal element gained the ascendency.

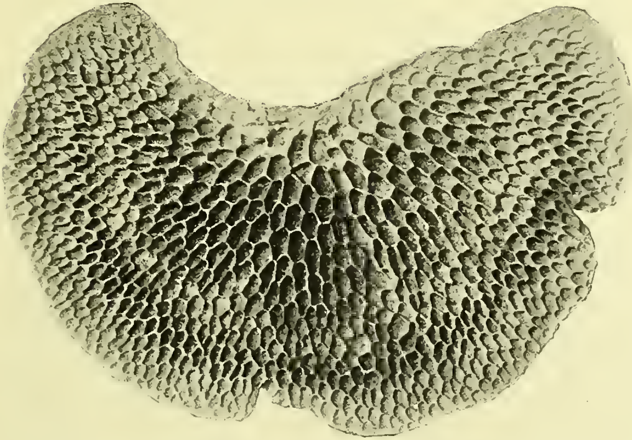

FIG. 48.—*Hexagonia apiaria*, a dry, coriaceous fungus belonging to the Polyporaceae, characteristic of tropical regions. Half nat. size.

Cooke has given us the nearest approach to a general distribution of fungi.

Berkeley and Broome, 'Ceylon Fungi,' coll. Thwaites, *Journ. Linn. Soc.*, 2, p. 494; 14, p. 29; 15, p. 82.

Berkeley and Curtis, 'Fungi Cubenses,' coll. Wright, *Journ. Linn. Soc.*, 10, p. 280.

Cooke, *Intr. to Study of Fungi*, p. 322 (1895).

Möller, 'Die Pilzgärten ein. südamerik. Ameisen,' in Schimper's *Bot. Mittheil.*, 6 (1893).

Möller, 'Brasilische Pilzblumen,' *Bot. Mittheil.*, 7 (1895).

Möller, 'Protobasidiomyceten,' *Bot. Mittheil.*, 8 (1895).

„ 'Phycomyceten u. Ascomyceten,' *Bot. Mittheil.*, 9 (1901).

ECOLOGY OF FUNGI.

The fact that fungi are dependent on organic matter for food debars them from becoming pioneers, and compels them to follow in the wake of chlorophyll-bearing plants, who directly or indirectly furnish such food. Obligate parasites are necessarily at the mercy of the host-plant. Saprophytes, as a rule, have a wider range than parasites, but in both instances there is evidence to show that there are some factors, at present unexplained, other than those exercised by host or merely apparently suitable conditions, which go to determining the presence or absence of fungi in a given locality. The survival of the fittest, or relative power to monopolise the situation, was very clearly demonstrated in the case of some mushroom beds I had an opportunity of examining. The beds, four in number, situated in an orchard, were prepared from the same manure heap, and stocked with spawn of the same quality obtained from one place only, in fact the whole of the spawn was broken up into pieces of the required size, and indiscriminately mixed before being placed in the beds. In due course two of the beds yielded an excellent crop of mushrooms, and judging from the method of preparation of the beds, as described above, all should have yielded an equally good crop; but such was not the case. In one of the unprofitable beds a strange toadstool appeared, which proved to be *Volvaria gloiocephala*, a pink-spored species. The first specimens of this intruder were removed, nevertheless it spread with amazing rapidity throughout the bed, and although a few small mushrooms appeared here and there, not a single marketable specimen was produced by the bed. In the second unprolific bed, *Clitocybe nebularis*, a white-spored toadstool, soon took possession, and no examples of the mushroom reached full growth. In both instances the mushroom proper was undoubtedly present in sufficient abundance to yield a good crop, but was simply stamped out by a better fighter. I have never observed, nor seen a case reported where a mushroom bed has been swamped by a species of *Coprinus*, belonging to the black-spored group of Agarics. As *Coprinus* grows normally and in immense quantities on manure heaps, it would at first sight have been expected that such fungi would have been the chief transgressors.

A probable explanation of the above is as follows. The Agarics are divided primarily into five groups depending on the colour of the spores, black, purple, brown, pink, white. I have elsewhere endeavoured to prove that the black-spored group is the oldest in time, and that the sequence of evolution of the groups is from black to white, the most modern group, in the order given. The only evidence in support of this idea bearing on the question under consideration is the practical absence of special contents, alkaloids, poisons of various kinds, corroding substances, etc., in the cells of the black group, and their gradual increase in number and potency, through the purple, brown, pink and white groups, in the last named being most generally distributed.

It is well known to every field mycologist that when a struggle between species belonging to different colour groups takes place, for a locality equally suitable to both so far as outside conditions are concerned, the white-spored species or its nearest ally invariably predominates over a member belonging to a darker-spored group. The white-spored *Clitocybe* and the pink-spored *Volvaria* respectively ousted the purple-spored mushroom from the beds. On the other hand, the purple-spored mushroom does not tolerate the black-spored *Coprinus* to encroach on its domain. Why this should be is not known; can it be due to the presence of some potent cell-content used by the higher fungi against the mycelium of the less perfectly protected lower groups? At all events this condition of things points to the fact that the monopoly of a given site rests more on the power of the parties competing than on external conditions. Either could be happy alone, but equal privileges are not tolerated.

On the other hand, fungi are not indiscriminately scattered, even in such a limited area as England. We have respectively characteristic upland, lowland, and swamp species. Apart from parasites the fungus flora of a pine wood differs from that of a beech wood or an oak wood. This, however, may be accounted for by the fact that the humus of a pine wood is different to that of a beech or an oak wood, or a pasture. It is within these areas, respectively furnishing all the requirements for a certain set of species, that the battles between differently coloured spore-groups take place.

Various species of *Boletus*, *Paxillus*, *Flammula*, and others, with coloured spores, are characteristic pine-wood fungi; in oak and other woods of broad-leaved trees, white-spored species predominate, whereas in pastures and open downs pink-spored species are common, as species of *Leptonia*, *Entoloma*, *Clitopilus*, etc.

The sporadic appearance of fungi is a fact well known to mycologists, and is not to be explained by climatic conditions. During certain seasons white-spored species largely predominate; during other seasons brown-spored representatives are most in evidence. In certain seasons some of the species generally most abundant and cosmopolitan are almost entirely absent. We are at present unable to offer even a suggestion for this condition of things.

PARASITES ON FUNGI

Fungi are by no means immune against the attacks of parasites which consist of other species of fungi. This is true of all the families.

In the Phycomycetes the species of *Mucor* are especially victimised; forms of *Piptocephalis*, *Chaetocladium*, *Dispira*, *Syncephalis*, and *Dimargaris* being among the parasites found on members of this genus, in all cases living on the sporangiophores.

Species of *Rhizidium*, *Olpidium*, *Pythium*, *Rozella*, etc., are parasites in the oospores, antheridia, or hyphae of various members of the Saprolegnieae.

In the Ascomycetes various species of *Peziza* are attacked by members of the genus *Bactridium*. *Cordyceps capitata* and *C. ophioglossoides* are parasitic on species of *Elaphomyces*.

In the Uredineae *Tuberculina persicina* is a parasite on various aecidium-forms, and *Darluca filum* infests sori of uredospores and teleutospores.

Among Basidiomycetes parasites are of frequent occurrence. *Hypomyces*, an ascigerous genus, occurs on various Agarics, *Polyporus*, *Boletus*, *Stereum*, etc. *Boletus parasiticus* grows on *Scleroderma vulgare*. *Pleospora clavariarum* occurs on various species of *Clavaria*.

Numerous fungi are parasitic on the apothecia and thallus of Lichens; these have been dealt with in detail by Zopf.

Zopf, *Nova Acta Nat. Cur.*, 70, p. 99 (1897).

PROTECTION OF FUNGI AGAINST SNAILS

Ludwig has obtained a red colouring matter from *Synchytrium* galls on *Anemone nemorosa*, which is readily soluble in water, and proves to be identical with anthocyanin. This substance is a derivative of tannin. He raises the question as to whether this substance is a purely pathological product, or whether it serves to protect the fungus against snails; pointing out Stahl's researches, which show how snails avoid plants producing tannin.

Ludwig, *Verh. bot. Ver. d. Prov. Brand.*, 31, p. 7.

Stahl, 'Pflanzen und Schnecken,' *Jena Ztg. für Natur und Medizin*, 22, N.F. xv., 1888.

FOSSIL FUNGI

Zeiller in a brief summary of the chronological sequence of fungi states that members of the Chytrideae, Mucoraceae, and Peronosporeae have been observed in vegetable tissues in Lower Carboniferous and Permian rocks.

Numerous Ascomycetes, Pyrenomycetes, and Discomycetes occur on leaves, and in the tissues and stems of many different plants, in some instances so well preserved that the structure of the perithecia with their conidia or spores can be studied. These extend from the Carboniferous period upwards. Members of the Hyphomycetes are also present during this period.

Basidiomycetes represented by members of the Agaricineae and Polyporeae have been found in Tertiary formations.

Zeiller also quotes Renault as announcing the presence of a member of the Uredineae occurring fixed to the inner wall of the macrospore of a *Lepidodendron* from the Lower Carboniferous period. The figure of a single body resembling a teleutospore, given by Renault, is, however, not convincing.

Weiss has notified the occurrence of a mycorrhiza in the root of what is probably a Lycopodiaceous plant, from the lower Coal measures. It is interesting to note that at this early period symbiosis between fungi and the higher plants was evolved.

Meschinelli has figured and described all known fossil fungi, numbering just over four hundred species.

Meschinelli, *Fungorum fossilium omnium Iconographia* (1898).

Weiss, *New Phytol.*, 3, p. 63 (1904).
Zeiller, *Éléments de Paléobotanique*, p. 37.

Massee, *British Fungi*, p. 212 (1891).

PERSONAL VIEWS ON PHYLOGENY

In the preceding pages I have endeavoured to give an idea of the various views respecting the origin and phylogeny of fungi, more especially from a cytological standpoint. What follows briefly represents my own view on the subject.

The idea of several, or at least more than one independent starting-point of fungi from algae does not commend itself, and morphological evidence is opposed to such a view.

In the evolution of aerial chlorophyllose plants from aquatic ancestors, the earliest form of male fertilising organ was a motile antherozoid, and this type remained in evidence so long as the evolving flora retained more or less of its original aquatic habit, and the sexual generation or oophore retained its independent individuality. As the flora gradually encroached on dry land, that is, as the facilities for fertilisation by antherozoids became less general, the individuality of the oophore became merged into that of the sporophore—a new factor evolved under changed conditions, and the motile antherozoid disappeared as a functional organ for ever. Now I presume that if there had been a later break from algae to form a second terrestrial group of chlorophyllose plants, the change would have taken place gradually, and that the first mode of fertilisation would have been of the ancestral type, by means of antherozoids, whatever line evolution might have eventually drifted into, depending on surroundings. But I believe there is no evidence of any such second break. It is important to keep in view the fact that the complete obliteration of the antherozoid, even after its period of functional value under the form of a motile organ had passed, was slow; nevertheless its presence in Gymnosperms does not prove that this group is anything more than one link in the chain of evolution of a single series of forms evolved from one break from the algae.

To my mind the fungi present a parallel case to the above. The Phycomycetes are most nearly in touch with the algae; there is the same general non-septate, vegetative structure, the same method of fertilisation, aquatic habit, and every character in common, save in the absence of chlorophyll in the fungi; this last feature in reality constitutes the only difference between many of the members of the Phycomycetes and such algae as *Vaucheria* and allied forms.

Long before we reach the end of the Phycomycetes or primitive group of fungi the effects of changed surroundings are observable, more especially in the gradual evolution of a new phase of development, analogous to the sporophore in chlorophyllose plants, for the purpose of utilising aerial conditions for perpetuating and disseminating the species. This new structure has received the name of sporophore or conidiophore, and the reproductive bodies borne by it are of asexual origin, as opposed to the sexually produced reproductive bodies borne by the primitive structure as it started from the algae. During the extension and differentiation of the Phycomycetes into genera the conidiophore phase became by far the most evident and constant feature, in fact most of the generic and specific characters are founded on it. It is interesting to note that even in the conidiophore or superadded phase the asexual reproductive bodies of the earlier forms produced motile zoospores, whereas in the more highly evolved and later types the homologues of the bodies that produced zoospores are transformed into what are termed conidia; that is, reproductive bodies distributed by wind, and which on germination produce germ-tubes or hyphae directly; hence during the accommodation of the Phycomycetes to aerial conditions the motile zoospore as an asexual reproductive organ is completely eliminated.

In proportion as the conidiophore phase of the Phycomycetes became differentiated, so the primitive sexual phase diminished in importance, and in some forms has entirely disappeared, the species being represented solely by its well-developed and characteristic asexual conidiophore condition. This gradual elimination of the primitive sexual stage is sometimes met with in different members of the same genus, as in *Phytophthora*, where in some species both sexual and asexual conditions are in existence, whereas in other species the asexual or conidiophore stage alone remains as in *P. infestans.*

During the evolution of the conidial phase a second new feature was added, the breaking up of the hyphae into cells by the formation of transverse walls or septa, a character which is continued henceforward throughout the entire group of fungi.

In the Phycomycetes there are two markedly different modes of sexual reproduction. In the Oosporeae section we have an antheridium and oogonium, exactly as in the algal ancestors, whereas in the Zygosporeae there is often no apparent sexual differentiation between the two gametes, and no receptive cell in the sense of a previously destined oogonium. Under the circumstances, either gametes originated as a modification of antheridium and oogonium respectively, or the conjugation by gametes was a new creation on the part of some of the Phycomycetes. Of course it may be suggested that the Zygosporeae are descended from algae like *Zygnema*. The whole question turns on this point. Is it possible for the same apparent type of sexual reproduction to appear at different periods of time, and in different groups of organisms, without implying phylogenetic affinity; or does the second appearance of a given type of sexual reproduction always imply phylogenetic affinity with the organisms furnished with an apparently similar type at a previous period? If phylogenetic affinity is implied, then we have indicated two, or probably three, independent origins from the algae in the group of fungi we call Phycomycetes alone. The Oomycetes would come from the Vaucheriae, and the Zygomycetes from Zygnemae. As to whether the sexual act in *Polyphagus* conforms with either of the above, is not certain.

Now in the Oomycetes, the most primitive group of fungi, we find the ancestral form of sexual reproduction by antheridia and oogonia, and the asexual method by means of motile zoospores. In this same group the conidial or asexual generation has gradually increased in complexity, and the original zoospore-producing fruit has changed to a body germinating by means of germ-tubes or hyphae.

Coming to the next group, the Mucorineae, we find the sexual reproductive bodies to be gametes, and the result of the sexual act a zygospore. Again, if phylogenetic affinity is implied by correspondence of sexual organs, the Mucorineae have descended from the algae known as Zygnemae. When we turn to the asexual form of reproduction in the Mucorineae, the gradual evolution of this generation, so observable in the Oomycetes, is absent. Zoospores are unknown, the conidiophores from the first are as highly organised as in the highest of the Oomycetes, and the reproductive bodies or spores contained in highly specialised sporangia seem to be derived directly from the simpler forms met with in the Oosporeae. In other words, the asexual or conidial generation in the Zygomycetes commenced where the same structure in the older Oosporeae left off, and continued evolving in accordance with the requirements of aerial surroundings. There is no starting-point of primitive simplicity in the conidial generation, as would be expected from analogy with the Oosporeae, if the Mucorineae had broken away independently from the Zygnemae.

Next in order come the Ascomycetes, characterised by having spores considered as the result of a sexual act, produced by free cell-formation within a mother-cell or ascus. In many species the sexual organs consist of an antheridium and oogonium as in the Oomycetes. But in numerous other species we are introduced to an apparently totally different type of sexuality. The male or fertilising element consists of minute non-motile bodies; these adhere to a more or less slender outgrowth of the female or receptive organ, called a trichogyne. Now this type of sexual organs resembles the one characteristic of the Florideae or red seaweeds at the present day, whatever it may have been in the remote past, when those fungi characterised by the presence of a trichogyne are supposed to have evolved from the Florideae. It so happens that those fungi possessing a trichogyne are amongst the most highly evolved, morphologically, of the Ascomycetes; amongst such may be enumerated *Polystigma*, *Poronia*, and *Xylaria*, all furnished with a complex stroma in which the perithecia are embedded. Some have conidial forms, others chlamydospores. We can beg a solution of this difficulty by assuming that all the primitive types of trichogyne-bearing fungi, that represented the first start from the Florideae, have disappeared, and that only the most highly evolved forms of this type remain. Or secondly, we may assume that this particular type of sexual structure appeared spontaneously in the fungi, without any connection with Floridean ancestors. But the matter does not end here. Blackman, as previously stated, has discovered traces of a rudimentary trichogyne in the Uredineae, and this he considers as suggesting close affinity with the Florideae. Blackman, however, denies any affinity between the Uredineae and the Ascomycetes; hence, according to him, the former did not derive their trichogyne from the latter. Here again we are reduced to the alternative stated above. Either the Uredineae represent a second new and independent origin from the Florideae, or the trichogyne, if it in reality exists, was a spontaneous development in the Uredineae. Finally, in Thaxter's Laboulbeniaceae, which he considers as belonging to the Ascomycetes on account of the sexually produced spores being formed in a mother-cell or ascus, the sexual organs are in absolute agreement with those of the Florideae, as is also the vegetative part, where protoplasmic continuity is so very conspicuous. This group, by common consent, is aloof from all other known Ascomycetes, and is yet further removed from the Uredineae, and therefore either represents a third independent departure from the Florideae, or a spontaneous evolution of a trichogyne.

It has already been stated that even in the Phycomycetes the original sexual phase showed a decline, and that in certain species it had completely disappeared, leaving the asexual conidial stage as the only representative of the species. This condition of things is much more emphasised in the Ascomycetes, where from the present standpoint of knowledge the great majority of species are asexual, in the sense of the sexual organs, when present, being no longer possessed of functional activity, whereas in numerous species the sexual organs are more or less rudimentary, or have entirely disappeared, and the structure producing spores that were originally of sexual origin remains in other respects unchanged.

It may perhaps be advisable to state that, taking the entire group of fungi into consideration, not more than a score of species are known to produce fruit as the result of a sexual act, that is, due to the fusion of a male and a female nucleus. All the rest is assumption or founded on analogy.

On arriving at the Basidiomycetes it is found that all trace of a sexual generation has completely disappeared, and the species as such consist of the conidiophore stage alone. This being the case the phylogenetic affinity of the Basidiomycetes cannot be determined from cytological evidence afforded by the sexual organs.

My idea of the evolution of the fungi is as follows, based on morphological evidence.

The Oomycetes section of the Phycomycetes are the most primitive of fungi at present known, and descended from a group of algae including *Vaucheria* and allies.

Conjugation by gametes, as met with in the Zygosporeae, is a modification of the older sexual form by antheridia and oogonia, inherited by fungi from the algae. In many species the two gametes are absolutely indistinguishable as to size or apparent function ; the transition from antheridia and oogonia is, however, indicated by such species as *Rhizopus nigricans*, where one gamete, the male, is much smaller than the other and remains unseptate. The much larger or female gamete has a septum formed near the free end which comes in contact with the male gamete, and this cut-off portion of the female gamete is the receptive cell, and eventually becomes the zygospore. The zygospore mode of reproduction had but a brief period of existence, and disappeared during the reign of the Phycomycetes.

The evolution of the conidial phase, with its septate mycelium and means of living in the air, must be considered as the first indication of an attempt to establish a definite group apart from the algae, and the two succeeding primary groups, the Ascomycetes and the Basidiomycetes, are simply extensions of this conidial phase, originating with the Phycomycetes. The old monosiphonous sexual stage, not being able to accommodate itself to aerial conditions, survived for a time, but could not emerge from the matrix or substratum, and did not extend beyond the Phycomycetes.

In the Ascomycetes both vegetative and reproductive portions are built up from the hyphae originating in the conidial condition of the Phycomycetes ; even the sexual organs, whether functional or effete, spring from distinctly septate mycelium.

In the Phycomycetes both sexual organs and conidiophores originate from the mycelium, hence there appears to be no objection to the assumption that the conidial condition of the Phycomycetes continued to produce antheridia and oogonia as it gradually evolved and passed into what is known as the Ascomycetes, through such groups as the Gymnoasceae. The hall-mark of the Ascomycetes consists in the presence of mother-cells or asci, containing the spores. The great advance of this method of reproduction over that of the Phycomycetes consists in the very much greater number of units—spores—each capable of producing a new individual, as compared with the sexually produced spores of the last-named family.

In the Phycomycetes the sexual act usually results in the formation of one spore, or its equivalent from the point of view of producing individuals; in *Pythium*, more than one, but never many, whereas in the Ascomycetes hundreds of spores may result. This is effected by the oospore, instead of ceasing its development soon after fertilisation, producing a variable number of outgrowths or hyphae, each of which gives origin to asci usually producing eight spores in their interior.

During the gradual extension of the Ascomycetes many new types of conidial fruit appeared. The oldest type, already evolved in the Phycomycetes as single erect hyphae, simple throughout or more or less branched upwards, and bearing a conidium at the tip of each branchlet, are much more complicated in the Ascomycetes, where the main axis of the conidiophore often becomes compound, or composed of an aggregation of hyphae grouped in different ways in different species, the tips of the hyphae spreading on every side, each tip bearing a conidium, or in several instances a long chain of conidia arranged like a necklace.

A second type of conidial fruit, previously unknown, appeared in the Ascomycetes, a characteristic example of which is to be seen in the form-genus *Phoma*. In this type the conidia are produced from the innermost cells composing a spherical, or flask-shaped, hollow body or perithecium, furnished with an apical pore or opening through which the conidia escape when mature. In many instances the structure of the perithecium is most elaborate and as nearly approaching to a parenchymatous structure as is to be met with anywhere in the fungi. Now if it is possible for the Ascomycetes to evolve a perfectly new type of perithecium containing asexual reproductive bodies, is it not equally possible to evolve a similar structure containing minute cells produced exactly like conidia in form and origin, but possessing the special function of male or fertilising bodies that become attached to and conjugate with a trichogyne? So far as the trichogyne itself is concerned it may be looked upon as merely a more or less elongated, and more or less slender outgrowth of the oogonium. Such a structure is present on the oogonium of *Pyronema confluens*. This type of sexual reproduction is only present in a degenerate form in the fungi proper, so far as at present known, but is of functional value in the fungal element of some lichens. This type is also present in the Laboulbeniaceae, but I am by no means satisfied that this group is an integral part of the fungi, notwithstanding the spores being produced in asci.

The last trace of sexual organs and the structures appertaining thereto disappear in the Ascomycetes, and the Protobasidiomycetes and the Basidiomycetes, which are strictly and absolutely conidial forms, I consider to have originated independently from conidial forms of the Ascomycetes.

Finally, as to Dangeard's idea respecting sexuality—as to whether it falls within the preconceived idea as to what actually constitutes a sexual act or not—I am not in the least concerned; to my mind the fusion of nuclei, as described by Dangeard, answers the purpose of a sexual act inasmuch as it imparts vigour or rejuvenescence. I fail to see that its efficacy is negatived by the fact that it occurs in some species where the older or acknowledged sexual method is yet present. It appears to simply signify that the newer (Dangeard's) method of rejuvenescence evolved before the older truly sexual method was completely obliterated, hence the two types overlapped. It is a parallel case to the coexistence of sexual and conidial forms; the original sexual type was destined to go, and the conidial state to take its place, and to give us the most highly organised and perfect forms, the Basidiomycetes. But the new or conidial type appeared long before the sexual stage disappeared, in fact the two stages overlapped to the end of the Ascomycetes. It is only the newest group, the Basidiomycetes, that is absolutely free from vestiges of the primitive sexual stage.

There yet remains to be noticed the enormous assemblage of forms usually included under 'Fungi imperfecti,' otherwise known as Hyphomycetes, Sphaeropsideae, etc. In many systems these groups are entirely ignored, presumably on the supposition that they are simply conidial forms of higher fungi. In purely systematic works these groups are included and treated, so far as descriptions are concerned, as entities or species.

Many of these species are probably only conidial forms or phases of ascigerous fungi; but there remain many hundreds that have not been proved by pure cultures, or even suspected from the standpoint of contiguity, to be associated with any higher form.

I incline to the opinion that in numerous instances the sexual stage has completely disappeared, leaving the conidial form alone. Assuming for the moment this idea to be correct, should such isolated conidial forms be considered as genuine species? All to whom I have put this question say, no!

Returning for a moment to the origin of the conidial generation, we find that it first appeared as a supplement to a sexual condition; the two phases might be in organic continuity, that is, originating from the same mycelium as in *Peronospora*, *Hypoxylon*, etc., or the two generations may be organically quite distinct, one generation originating from the mycelium formed by reproductive bodies produced by the other generation, as in *Sclerotinia*, where Woronin has shown that certain species are even heteroecious. Now in these examples the conidial form is not an entity, but, along with the sexual phase, constitutes a species.

As previously noted, even in the earliest group, the Phycomycetes, the sexual phase was on the wane; I believe it to be generally accepted that the sexual phase of *Plasmopara infestans* has disappeared, the conidial phase only remaining, yet I am not aware that any one has objected to this conidial form being accepted as a species, or that any one has suggested its removal to the Hyphomycetes, to which group technically it belongs. Numerous other accepted species included in the Phycomycetes are only represented by the conidial phase. Now this must surely be wrong if a conidial condition cannot be accepted as a species.

Then again, to be consistent, what is the status of the enormous assemblage of typically conidial forms collectively constituting the Basidiomycetes? These are all accepted as species, which, if a conidial form cannot be so termed, is again a mistake.

It is important to bear in mind that in the sexual generation the reproductive bodies are the result of a sexual act, or, at all events, were once sexual in origin, even if at the present day its sexual organs are effete; in the conidial generation the reproductive bodies are asexual in origin.

The sexual generation was dominant in the most primitive groups of fungi, whereas the asexual or conidial phase was intermittent. In the latest group of fungi the asexual or conidial phase is universal, and the sexual generation absent. This change was probably rendered possible by the evolution of Dangeard's conjugation of nuclei at a certain phase of development, which completely superseded the original sexual method; and which, whether technically sexual or not, effects the object of imparting rejuvenescence, and the ability to become cosmopolitan on the part of those groups dependent on this method alone.

As to whether the ascigerous fruit in the genus *Hypomyces* is the result of a sexual act is not known, but I have shown that its conidial phase, known as *Mycogone*, has the vegetative cells binucleate, and further, that in the conidium the two nuclei fuse. This is Dangeard's idea of a sexual act; however, apart from this special point, the fact remains that this method of rejuvenescence may already exist in the conidial form of a species which yet retains the older ascigerous form of fruit.

If we once more contrast the evolution of chlorophyll-bearing plants with that of the fungi, the superiority of the former from both a morphological and physiological standpoint is at once evident, as compared with the fungi. In both groups the primitive sexual generation—as a distinct and independent structure—has gone in the higher forms, but in chlorophyllose plants it was, as it were, absorbed by the newer sporophyte generation, and its primitive functional activity retained. It is this retention of the means of sexual reproduction that has enabled the sporophore generation of chlorophyllose plants to attain their present development. Ample proof of this idea is illustrated by the difficulty experienced in perpetuating plants reproduced by asexual or vegetative methods alone, as potatoes, etc.

The fungi, on the other hand, through inability to incorporate the sexual phase with the new aerial conidiophore, have failed to evolve morphologically beyond the primitive hyphal element; there is no vestige of a tissue, as understood in phanerogamic structures, present in the highest forms. The evolution of nuclear fusion, as demonstrated by Dangeard, has saved the fungi from actually disappearing, but it has proved incapable of enabling them to assert themselves, thus demonstrating its inferiority as compared with true sexual reproduction.

II. PATHOLOGY

DISEASE CAUSED BY FUNGI

Obligate parasites have been shown by Brefeld to be not under all conditions absolutely dependent on the presence of a living host for their development. He succeeded in growing members of the Ustilagineae in nutrient media under special conditions. On the other hand, I have succeeded in inducing fungi only known in nature as pure saprophytes to become true parasites. Notwithstanding the above and much more evidence in existence on the same subject, I am more than doubtful as to whether such evidence is in reality as convincing as it appears to be at first sight.

It is always the outcome of so-called pure cultures, and this fact alone suggests to my mind—when dealing with fungi—a suspicion of doubt, not doubt as to the fact of its being a pure culture ; this point with present day appliances can be assured. The doubt arises from the conditions under which pure cultures are—at present—necessarily conducted. Suppose an infection experiment on a given plant is the object in view, to secure an uncontaminated host, the seed is sown in sterilised soil and placed under a bell-jar, which is never removed except for a moment when the spores of the fungus are placed on the young plant. Is such a host normal in every respect? Would a gardener desiring healthy, hardy plants, of the kind experimented with, grow them under those conditions? It is very doubtful whether the physiological condition of the host-plant under such abnormal conditions can be similar to those of a plant of the same kind grown under normal conditions, and if this be true, to what extent does the experiment teach us as to what takes place under natural conditions?

The result must necessarily be less convincing when detached parts of plants or even isolated leaves are used for pure cultures. Under such conditions it is difficult to conceive that the varied constituents of the cells continue to be similar in every respect to those still attached to the parent plant. Such experiments are undoubtedly instructive, and show the reciprocal influence of parasite and host respectively under a given set of conditions, which is perhaps as far as we are really justified in assuming. Probably every one will agree to the statement that plants experimented upon, when grown under the conditions enumerated above, are in that state which common experience has long ago proved to be the one most susceptible to infection and disease.

The only hope for a final solution of the intricacies connected with diseases of plants caused by fungi, nay, of disease in general, appears to depend on a fuller knowledge of physiology and bio-chemistry.

The knowledge possessed at the present day appears to favour the idea that parasitism in fungi is an acquired habit. This idea is supported by the cases recorded above, also by the fact that the numerous fungi known as facultative parasites can live equally well either as saprophytes or as parasites.

It is not intended in this place to discuss the complicated problem relating to disease; those desiring information on this point should consult Ward's masterly treatise on the subject, entitled *Disease in Plants.*

It is almost impossible to conceive any living organism being placed under such conditions, that it is supplied with all the requirements, and at the same time protected against all harmful influences, necessary to ensure perfect development. In proportion as a living body recedes from this ideal condition, so its power of self-protection may possibly, but not necessarily, become lessened, and the influence of its departure from the mode of life normal

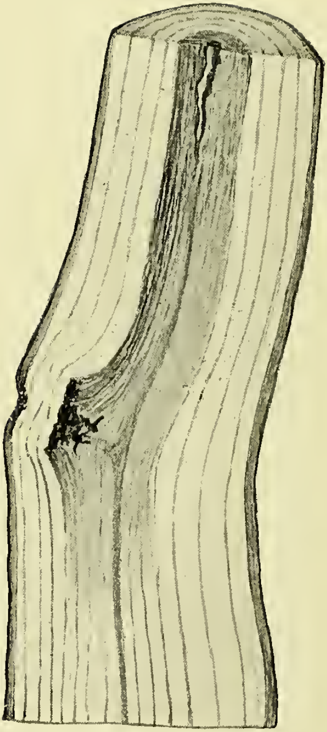

Fig. 49.—Section of portion of the stem of a young apple-tree, showing the effect of pruning and not protecting the cut surface. The dark portion is diseased owing to a parasitic fungus having entered the tissues through the unprotected wound. The tree died due to the spread of the fungus in its tissues some years after it was attacked. Fig. reduced.

to the species may incline it to a greater susceptibility to disease; that is, it may have less power of resistance against external influences injurious to itself. Fungi must always be reckoned amongst such external factors where plants are concerned, and many fungi appear to be only able to attack plants that are below the normal in vigour. Other fungi attack plants more especially when life is on the wane, as fading leaves, nearly ripe fruit, etc.

FIG. 50.—*Rhytisma acerinum*, a parasitic fungus forming black patches on a living sycamore leaf; 2, section through a portion of a black patch or stroma bearing spermatia or conidial form of fruit; 3, ascus containing eight needle-shaped spores, and accompanied by two slender curved paraphyses; 4, a free ascospore. The ascospores are produced in the spring, after the dead leaf has been lying on the ground throughout the winter. Fig. 1, one quarter nat. size; figs. 2-4, highly mag.

FIG. 51.—*Peronospora viticola*, a parasitic fungus very destructive to the vine. 1, white patches of the conidial form of fruit on a vine leaf; 2, group of conidiophores issuing through a stoma and bearing conidia; 3, three conidia; 4, conidia producing zoospores, in *a*, the zoospores are yet within the conidium; *b*, two zoospores that have escaped from the conidium; 5, mature oospore or resting-spore; 6, an oospore germinating and producing the conidial form of fruit; 7, autumnal form of shortened conidiophore bearing a few large conidia. Fig. 1, reduced; the remainder highly mag. (Figs. 6 and 7 after Prillieux.)

On the other hand, many plants that are presumably healthy and robust are attacked by true parasitic fungi;

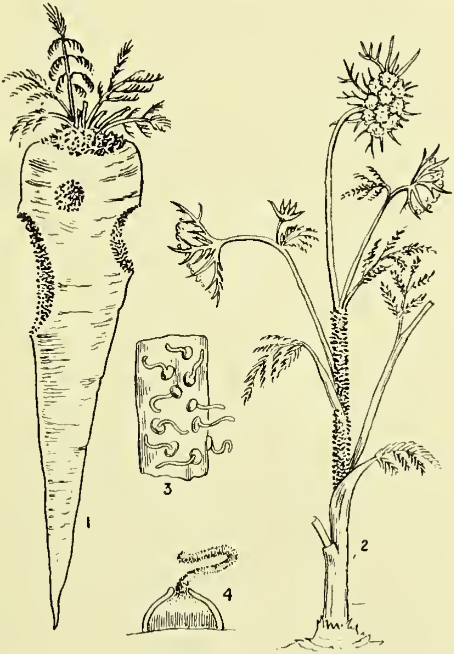

FIG. 52.—*Phoma sanguinolenta*, a fungus belonging to the Sphaeropsidiaceae, parasitic on carrot. 1, a carrot root attacked and partly eaten away by the fungus; 2, stem of carrot attacked by the fungus; 3, portion of a diseased spot showing perithecia with the conidia being discharged in tendrils; 4, section of a perithecium with the conidia oozing out as a gelatinous tendril. Figs. 1 and 2, reduced; figs. 3 and 4, highly mag.

among such are all the members of the Uredineae, the Ustilagineae, and many species belonging to the Ascomycetes, as *Polystigma rubrum*, forming reddish thickened blotches on the leaves of various rosaceous plants, and *Rhytisma acerinum*, forming large black blotches on the leaves of sycamore and maple. The whole of the Erysipheae, which cover living leaves with a white mildew, also belong to this category.

Parasitic fungi affect the host-plant in different ways. Some species, as *Phytophthora infestans*, the cause of the too well-known potato disease, in severe cases, or in other words, when climatic conditions favour the parasite, kills the host-plant within a very short space of time. *Pythium debaryanum*, the cause of damping off in seedling plants, acts in a similar manner. Trees are also soon killed when the roots are attacked by *Agaricus melleus*, or by species of the Ascomycete called *Rosellinia*.

Other fungi, as *Rhytisma*, *Polystigma*, and numerous other species belonging to the Ascomycetes, Sphaeropsideae, etc., only cause local death, that is, the mycelium only extends for a short distance from the point of infection, the result being the destruction of a small patch of living tissue. Many of the dead patches on otherwise living and vigorous leaves are caused by parasitic fungi, the minute fruit of which is situated on the dead patch or immersed in the tissue.

Proceeding one step further we come to a group of fungi which, after inoculation, live in the tissues and at the expense of the host for a considerable length of time without, so far as we know, inflicting the slightest injury or inconvenience, and whose presence is not revealed by any outward sign, the host continuing to grow in a perfectly normal manner. The members of the Ustilagineae are past masters in this method of parasitism. Sedges and grasses are their victims, and in many instances the host can only be infected in the youngest seedling stage, the

FIG. 53.—*Ustilago avenae*, one of the Ustilagineae causing the disease known as 'smut' in oats. 1, a 'smutted' ear of oats; 2, spores; 3, spores germinating and producing minute secondary spores which again reproduce themselves by budding or gemmation, after the manner of yeasts; 4, secondary spores conjugating in pairs. Fig. 1, reduced; the remainder highly mag.

mycelium of the fungus spreads in the tissues and keeps pace with the growing plant, where it remains for months, and only reveals itself during the last stage of the life of the host, as a sooty mass of spores in the anthers, ovary, etc. As a rule, when an ear of oat is smutted, all the grains are destroyed, but sometimes a few grains escape and develop in a perfectly normal manner, thus proving that notwithstanding the presence of the parasite from its birth, the host has been able to run its normal course of life, even to the production of perfect seed. Obviously an infected oat plant has to work a little harder than an uninfected one, as it has to provide food for its parasite as well as for itself. This condition of things appears to be a leading up to symbiosis, falling short owing to the fact that there is no obvious benefit derived from the union by the host, but the reverse; hence the parasite is as yet dominant.

In the remarkable growths often present on the branches of trees, more especially conifers, but also on cherry, birch, etc., known as 'witches' brooms' or 'birds' nests,' the suggestion of symbiosis is yet more evident. Witches' brooms possess some common characteristics. When a branch of a tree is infected, most frequently by some member of the Uredineae, the stimulation exercised by the parasite results in an excess of food being concentrated at the point of infection. This leads to the formation of a dense mass of branches, themselves usually copiously branched, being produced at this point and constituting a witches' broom, which may equal in size and appearance a crow's nest, and in many instances where such growths are of considerable age this size is much exceeded.

The general habit and mode of life of a witches' broom is in all cases very different from those of the parent plant from which it springs. Its branches are always vertical or very strongly negatively geotropic, whereas the parent branch from which it originates is horizontal in conifers, and more or less so in other trees. This erect habit causes the witches' broom to stand out conspicuously, and to resemble an alien. All the branches of the broom are permeated with the mycelium of the fungus throughout. The leaves are always annual in duration, small in size as compared with those of the parent tree, almost devoid of chlorophyll, and bear the aecidial or 'cluster-cup' fruit of the fungus. After the spores of the fungus are shed, the leaves fall, quite early in the season. No fruit is produced by a witches' broom. Owing to the absence of chlorophyll a witches' broom is unable to supply itself with food, and is practically a parasite on the parent plant to the same extent, or even more so than a mistletoe would be. The broom and its parasite are very nearly in a symbiotic condition, the fungus derives its food from the broom, and the latter in turn depends for its food on the stimulation exercised by the fungus on the parent plant. Symbiosis is not yet complete, for although there is mutual benefit, and the compound structure may continue growing for many years, the fungus is yet dominant, as the host is modified adversely to the extent of not being able to reproduce itself.

It may be well to state that many witches' brooms, indistinguishable so far as general appearance goes from those described above, owe their origin to members of the animal kingdom, mostly microscopic mites belonging to the genera *Phytoptus*, *Eriophyes*, etc. Such brooms are common on silver birch, alder, etc.

Diseases induced by fungi often cause very remarkable modifications in form and structure of the host-plant. Such may be briefly alluded to under two headings.

(1) Atrophy. Reduction in size or abortion of the plant, or of special organs. Fungi causing this condition of things have been termed Atrophytes. The stunted leaves of witches' brooms illustrate the arrest of development of a special part of the plant. A minute fungus called *Synchytrium*, forming tiny galls on leaves of dandelion and other plants, prevents such leaves from attaining the normal size. Sometimes the entire plant is much stunted, as in the case of *Euphorbia cyparissias* when attacked by the aecidial form of *Uromyces pisi*. Here the stunting is so marked that there is not the slightest resemblance to normal plants of the same species. When *Agrostis vulgaris* is infected with *Tilletia decipiens* the whole plant is much dwarfed, and was at one time considered as a distinct variety called *pumila*.

(2) Hypertrophy. An abnormal enlargement of an organ or of the entire plant. Fungi causing such abnormalities have been termed Hypertrophytes. Members of the Uredineae often cause a considerable increase in size of the parts infected. *Gymnosporangium* causes spindle-shaped swellings on branches of juniper, and also very large barrel-shaped thickenings on the trunks of various conifers. Galls reaching to the size of a cherry are formed on the leaves of *Rhododendron hirsutum* by a species of *Exobasidium*. Branches of *Acacia horrida* are much swollen and twisted into most fantastic shapes by a fungus called *Aecidium ornamentale*. *Ustilago cruenta* causes the stem of *Zizania latifolia* to become swollen and succulent, and in this condition it is sold as a vegetable in China. In Northern Europe young shoots

of spruce are often attacked by a fungus called *Peridermium coruscans*; as a result the leaves become shorter and succulent, and in this condition have been used as food.

As would be expected when such distortion takes place, the microscopic structure is much disturbed, certain systems of tissue are developed in excess, whereas others are equally arrested. A detailed account of such changes is given by Küster.

FIG. 54.—*Exobasidium rhododendri*, a primitive type of a basidiomycete parasitic on leaves of *Rhododendron ferrugineum*, where it forms large galls. 1, branch of *Rhododendron*, with galls on the leaves formed by the fungus; 2, basidia of the fungus bearing a variable number of spores. Fig. 1, reduced; fig. 2, highly mag.

Although saprophytic fungi do not injure living plants, nevertheless many such are of economic importance, and rank amongst the most destructive of fungi. 'Dry rot' caused by *Merulius lacrymans*, a true saprophyte, is an example. Some saprophytic species of *Polyporus* are also destructive to worked wood.

Members of the animal kingdom are by no means exempt from the attacks of fungi. Insects are perhaps the greatest sufferers, and more especially in the larval condition are destroyed in immense numbers. The various species of *Cordyceps* confine their attention to insects; after infection, the larva, or in some instances the perfect condition of the insect, continues to live for some time; finally it succumbs, and its body becomes filled with a dense mass of interwoven hyphae, a sclerotium in fact. In due course the exterior of the mummified insect becomes covered with the conidial form of the fungus—constituting the form-genus *Isaria*—and at a still later stage the ascigerous condition is developed under the form of one or more club-shaped bodies. The dead bodies of larvae, more or less buried in moss and bearing the pale yellow silky clusters of conidia, or the crimson club-shaped ascophores of *Cordyceps militaris*, are not uncommon in this country. A species of *Saprolegnia* is the cause of the destructive salmon disease; other kinds of fish also suffer.

Human beings are by no means exempt from diseases due to fungi, and in too many instances suffer from such at a very early age. 'Thrush,' the white pellicle on a baby's tongue, gums, etc., is caused by *Oidium albicans*. 'Ringworm' is caused by *Achorion Schoenlenii*. Numerous other examples are on record.

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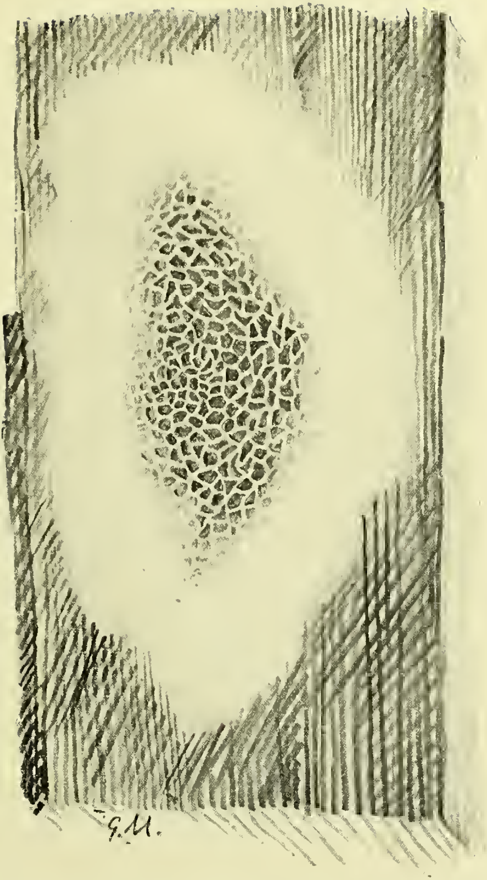

FIG 55.—*Merulius lacrymans*, the 'dry rot' fungus, which is not a parasite, but is very destructive to worked wood. One quarter nat. size.

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THE SPREAD OF DISEASE BY MEANS OF HYBERNATING MYCELIUM

Until recently it has been assumed that the great bulk of disease caused by fungi was due to the infection of the host-plant by means of spores. This idea to a great extent is quite correct; nevertheless recent research has demonstrated the fact that in many of the most destructive diseases spores play but a small part, and in some instances no part at all, in the perpetuation of such diseases. Of course it has long been known that certain kinds of fungi produce sclerotia, or concentrated masses of mycelium, which are capable, after a period of rest, of propagating the species independent of spores; again, some kinds of fungi produce long strands of mycelium, which either extend for a considerable distance under ground, as in the case of *Agaricus melleus*, or in the humid forests of tropical regions certain species of *Marasmius* often form a dense tangle of fine threads, that might be mistaken for a growth of *Cuscuta*, or dodder, on the branches of shrubs. These strands of mycelium give origin at intervals to clusters of sporophores, often at a very considerable distance from the parent stock.

Apart from such exceptions, all attempts to check the extension af parasitic fungi injurious to cultivated plants have turned on some method for destroying the spores; such lines of treatment being based on the assumption that the plant to be protected was free from disease until infected from without by means of spores.

As previously stated, this assumption has been shown to be too sweeping, and in reality in many instances spores play a very subordinate part in the perpetuation of a disease; their part being taken by hybernating mycelium present in the seed, tuber, bulb, or whatever portion of the plant serves for the purpose of reproduction. More than this, it has been proved that when a plant is once infected, the mycelium present in the seed, tuber, etc., grows along with plant, extends to the above-ground portions where, in due course, spores are often produced;

but, what is more important to remember, the mycelium also extends into the seed or tubers of the growing plant, consequently the offspring of that particular plant is infected for all time without the fungus ever leaving the plant, and quite independent of spores. The spores produced on the above-ground portion of the diseased plant serve to infect other plants of the same kind, thus securing an even greater extension of the area of disease caused by the particular species of fungus.

The discovery of this method of propagating a disease by means of hybernating mycelium present in the reproductive portion of the host-plant, explains the failure to check certain diseases by means of spraying, and also explains the sudden appearance of a disease in a new district when seed assumed to be free from infection was used.

The same discovery also suggests the probability that the sudden appearance of an epidemic, previously assumed to be due to the rapid production and diffusion of spores, may in reality not be dependent on the presence of spores at all, but rather to the presence of hybernating mycelium, which, under favourable weather conditions, developed rapidly and set up an epidemic.

Infection by means of spores is the most primitive and most general method followed by fungi ; what may be termed the more modern method of infection by means of hybernating mycelium is quite as effectual, and much more economical. When the balance between fungus and host-plant is perfect, infection, by means of hybernating mycelium, which passes from one generation to another without ever leaving the host-plant, is rendered so certain, that the production of spores is completely arrested.

The following examples of the method of perpetuating a disease by means of hybernating mycelium serve to illustrate the gradual obliteration of spores as a means of infection :—

(1) Both spores and hybernating mycelium in the seed are necessary.

This illustrates the least differentiated attempt to perpetuate a disease by means of hybernating mycelium.

Examples.—'Smut,' caused by species of *Ustilago*, in some cereals and other grasses.

(2) Hybernating mycelium alone is capable of perpetuating the disease from one generation of the host-plant to another; spores, however, are as yet produced, which by their diffusion inoculate other plants, and thus serve to extend the area of the fungus.

Examples.—'Potato blight,' caused by *Phytophthora infestans*, and potato 'leaf-curl,' caused by *Macrosporium solani*.

(3) Hybernating mycelium located in the seed is alone present.

This phase illustrates the perfection of the modern method of infection and dispersion of a fungus by means of hybernating mycelium. The ancient method of infection by means of spores has been completely obliterated.

It has been assumed up to the present that the infection of cereals by 'smut' (*Ustilago*) spores could only be effected during the earliest seedling stage of the plant. Such infection was considered to be effected by spores present in the soil, or more generally by smut spores adhering to the 'seed' and sown along with it. As a preventive against such infection, it is the common practice to treat 'seed' before sowing with a solution of formalin, sulphate of copper, or some other fungicide. Such treatment sometimes proves beneficial, sometimes not.

Brefeld has recently published an account of his investigations on the infection of cereals and other plants by 'smut' (*Ustilago*) spores. As the result of numerous experiments he has proved that in the case of wheat, barley, and certain other plants of no economic importance, infection takes place through the flower, and not during the seedling stage in the ground. Spores carried by wind, insects, or in the case of aquatic plants by water, are deposited on the stigma, where they germinate and pass down into the ovary or young seed. There a certain amount of hybernating mycelium is formed which remains in a resting condition until the seed is sown, when the mycelium grows along with the plant, and finally produces the well-known sooty mass of smut spores in the seed.

In this instance it will be observed that infection takes place in one generation, and the fungus produces fruit in the next generation of the host-plant; the interval having been tided over by the presence of hybernating mycelium in the 'seed.' Spores are, however, necessary to secure infection in the first instance.

Brefeld showed that oats and some other plants can only be infected during the seedling stage, by spores present in the soil.

Farmers are well aware that, by proper treatment of the 'seed,' smut can be reduced to a minimum in the case of oats, whereas smut in barley cannot be prevented by the same line of treatment. Brefeld's discovery has furnished the explanation. Smut in oats is the outcome of infection during the seedling stage, due to the presence of spores adhering to the seed. Hence, if such seed is treated, the spores are destroyed. On the other hand, in the case of barley, infection takes place through the flower; hence treatment of the seed is of no avail.

Potato growers have for some time past expressed the opinion that infection by spores alone appeared inadequate to account for sudden waves of potato disease appearing simultaneously over a wide area.

Various experiments have been conducted at Kew with the object of determining the different modes of infection of potato tubers. The following, among others, is considered as affording definite evidence as to the existence of hybernating mycelium of potato blight (*Phytophthora infestans*), and potato leaf-curl (*Macrosporium solani*) in potato tubers, capable of imparting the disease to the offspring of the infected tuber.

Three potato tubers showing the rusty stains indicative of the presence of *Phytophthora* mycelium in the flesh were each cut into two equal parts. Each half tuber was planted separately in a plant pot. The soil and manure used was of the same kind for all, and was sterilised by steam. Three of the pots were placed in a house having a temperature ranging between 70° and 80° F., and very often the moisture was at saturation point. Each pot was covered by a bell-jar. The three remaining pots were placed in a house without any artificial heat, and having the air exceptionally dry. These pots were not placed under bell-jars. An equal amount of water was supplied to each of the six pots. The three plants grown under conditions of high temperature and much moisture grew quickly and were much 'drawn.' The *Phytophthora* first appeared when the shoots were six weeks old, and a fortnight later all three plants were blackened and destroyed by the fungus. The three plants grown in the cool, dry house showed no trace of disease at the end of two months. At this time one of the plants was removed from the cool to the hot, damp house, and placed under a bell-jar. Within nine days this plant was blackened and killed by the fungus. A fortnight later a second plant, showing no trace of disease, was removed from the cool to the hot, damp house and placed under a bell-jar. Within a week this plant was also killed by a copious growth of *Phytophthora*. The third plant was kept for thirteen weeks in the cool house, and remained perfectly free from obvious disease.

Similar results were obtained by planting potato tubers produced by a plant badly infected with potato leaf-curl (*Macrosporium solani*).

Although hybernating mycelium is present in tubers, and consequently capable of continuing the disease from one generation to another, yet spores are also produced in abundance; these spores infect other plants, and thus constantly add to the number of permanently infected tubers. The fact of spores being produced accounts for the benefit derived from spraying. Such benefit is in proportion to the amount of injury that would follow infection by spores. The spraying would be without action on the amount of damage caused by the hybernating mycelium.

The above experiments also prove another point of great importance, namely, that the appearance of an epidemic of potato blight depends almost entirely on weather conditions.

In the experiment described it was known that all the potatoes were diseased, but in the case of those grown in the cool house, and in a comparative absence of moisture in the air, the fungus was held in abeyance, and a crop grown under such conditions would have matured without a trace of obvious disease, although the disease known to be present quickly manifested itself when the plants were placed under conditions that favoured the rapid development of the fungus. On the other hand, in the three plants that were grown under conditions specially favourable to the fungus, the disease quickly manifested itself. The same relative conditions occur in nature. Every grower of potatoes can predict with almost unerring certainty the advent of potato blight, the sign being damp, warm, cloudy weather. Under such conditions it is highly probable that the sudden outbreak of disease is not the result of infection by spores, but rather due to the presence of the fungus already in the plant, that originated from hybernating mycelium, suddenly stimulated to action by favourable weather conditions.

In many instances, more especially in the Lichens, the balance between parasite and host has become so thoroughly adjusted that no injury is experienced by either component; on the other hand, mutual benefit is derived from the combination. When this condition of things is attained it is expressed by the term symbiosis or mutualism. Symbiosis between fungi and flowering plants is not common, but a striking instance is recorded by Freeman as existing between certain fungi and three kinds of rye-grass respectively, *Lolium temulentum*, *L. perenne*, and *L. italicum*. In *L. temulentum*, or darnel, the life-history of the fungus is briefly as follows. The mycelium of the fungus is present in the 'seed'; on germination this mycelium also commences growth, and keeps pace with the host-plant, finally again entering the seed, where it remains in a resting condition until the 'seed' commences to germinate, when the same cycle is repeated. A series of experiments proved that infected plants were more vigorous than uninfected ones. So certain is the fungus of perpetuating itself by this vegetative method, without ever quitting the host-plant, that the production of spores has been completely arrested, hence there are no means of ascertaining with certainty the affinities of the fungus.

In the absence of spores no other plants of the same kind can be infected, consequently there exist two races of each of the three kinds of rye-grass, one race infected with a fungus, the other race uninfected, and without a possibility of becoming infected. Microscopical examination of a commercial sample of darnel 'seed' showed over eighty per cent. to be infected.

Many other instances could be enumerated where disease is perpetuated from generation to generation by means of perennial mycelium, but perhaps sufficient has been written to show that this method of disease perpetuation and distribution is a factor not to be ignored, and that it probably plays a much more prominent part in these directions than is generally supposed.

LEGISLATION, AND THE SPREAD OF PLANT DISEASES CAUSED BY FUNGI

It is well within the mark to state that the annual loss throughout the world, due to injury caused to cultivated plants by parasitic fungi, exceeds £150,000,000 sterling. Probably double this amount would be nearer the truth.

The following specific cases may be quoted in support of this statement.

According to the Prussian Statistics Bureau, the losses in Prussia during the year 1891 from grain rust attacking wheat, oats, and rye, amounted to £20,628,147. The Year-Book of the United States Department of Agriculture for 1897 estimates the injury caused by fungi during that year in the United States as amounting to about £40,000,000. In Australia the loss in the wheat harvest of 1890-91, on account of rust, was estimated at £2,500,000. Data of a similar nature for this country are not forthcoming, but our average annual loss is probably not less than that of other countries, as mildew, rust, etc., are always more or less in evidence.

Can this serious annual loss be prevented, or reduced in amount, is the question which naturally suggested itself.

Undoubtedly yes, as proved by results obtained, more especially in the United States, and in some European countries; but, speaking broadly, attempts in this direction have been confined to checking the spread of a given disease, after its appearance, and as such have not touched the root of the matter. The primary cause must be removed before any enduring benefit can result. Legislation has also been called in aid, but again, as will be shown, minor details have received much consideration, whereas broad, underlying principles have been overlooked.

It is a well-known fact that diseases are constantly appearing in new localities, and a point of primary importance is to determine with certainty by what means such diseases are conveyed. This subject can be most conveniently discussed under two distinct headings, as follows.

1. Diseases that appear when the host-plant is introduced

to distant localities, even to a new continent, where the fungus was not known to exist previous to the introduction of its host-plant.

2. Diseases that spread from an area known to be infected, to adjoining areas hitherto free from disease.

Instances falling under No. 1 will first be given.

Previous to the introduction of wheat into Australia, the wheat rust fungus (*Puccinia graminis*) was unknown in that country, but almost at once, after the cultivation of wheat commenced, rust appeared in full force; and at the present day wheat in Australia suffers as much from rust as in any other part of the world.

The Hollyhock, imported to Europe from Chile, was followed by its natural enemy, Hollyhock rust (*Puccinia malvacearum*), which not only at one time threatened to exterminate this plant in Europe, but has also attacked all European wild species of plants allied to the Hollyhock.

Quite recently diseased specimens of French beans were sent to Kew for investigation from the Botanic Station, Mairobi, British East Africa. It was stated that the plants had been grown there for the first time, and promised to yield a good crop, when they were suddenly all destroyed by some disease. On investigation it proved that both the leaves and fruit were attacked by the same kind of fungus respectively, from which they so frequently succumb at home; the parasite on the leaves being *Uromyces phaseoli*, that on the fruit was *Colletotrichum lindemuthianum*. Lucerne suffers in America, Australia, and the Transvaal from the same kind of fungus that destroys it in Europe. Maize smut is now common in Europe. Seedlings of *Verbena* raised in Brisbane have been destroyed by the same kind of fungus attacking Verbenas in Europe. These are a very few of the cases that could be cited where European plants that have been cultivated in distant parts of the world have been attacked there by the same kind of fungus from which they suffer at home.

A point of importance in connection with the above examples is the fact that, in every instance, the introduction to a new country must necessarily have been by means of *seed.*

Next comes the question : How did these plants become infected in the first instance in a new country, with the same kind of fungus from which they had been accustomed to suffer at home?

Two possible answers suggest themselves. Either the fungus was previously present in the new country, and happened to be growing in the immediate neighbourhood where the introduced plants were first grown. Or, secondly, the spores of the fungus were imported along with the seed, adhering to its surface.

The first supposition may be dismissed at once, as not having a shred of evidence in its support. The latter supposition is strongly supported by facts, and may without doubt be accepted as the true solution. It has long been known that smut and bunt in cereals are mainly perpetuated by the spores of these fungi adhering to the outside of the grain, and that by proper treatment the spores can be destroyed, a practice commonly followed. This method of treating seed before sowing could be greatly extended with advantage.

Packets of a dozen different kinds of seed purchased at random were carefully examined in the Jodrell Laboratory at Kew, and in four instances, spores of the fungus, well known as causing a disease on the plant in question, were obtained from the seeds.

The theory that fungus spores may be carried by air currents for long distances, even from Europe to Australia, cannot be entertained.

Now, in the case of seeds, legislation has played little or no part, yet it is almost certain that many of the most destructive diseases have been introduced into new areas through the spores of the fungus adhering to seed.

A second source of dispersion of disease, which in these days of rapid transit is easily accomplished, is where the mycelium of a parasitic fungus hybernates in the vegetative portion of a plant that is used for reproduction in place of seed. Tubers and bulbs may be cited as examples.

It is well known that when potatoes are attacked by 'potato blight' (*Phytophthora infestans*), the tubers are usually more or less diseased, the external indication of which is the presence of brown stains in the flesh of the tuber. If a browned portion of a tuber is examined under the microscope, the living mycelium of *Phytophthora* can always be found; in fact the mycelium of the fungus is the definite cause of the browning. The point to bear in mind is the fact that if such a diseased tuber is planted, the mycelium present in its substance grows into the young sprouts, follows up the inside of the haulm, and finally appears as 'potato blight' on the leaves, if conditions are favourable for its development. It may be argued that obviously diseased potatoes would not be planted; perhaps not, but potatoes often contain the mycelium of *Phytophthora* when there is no evidence in the way of discoloured blotches on the surface, and but scanty naked-eye evidence when cut. Nevertheless the comparatively small amount of living mycelium present may suffice for continuing the disease in the way indicated above. It is more than probable that in many instances the rapid spread of disease in a potato field, usually attributed to the conveyance of spores from diseased to healthy plants by wind, rain, movements of animals, etc., is in reality due to the fact that slightly diseased tubers have been planted; and that under those atmospheric conditions so well known as being favourable to the appearance of potato blight, the disease already lurking in the haulm, and having originated from the tuber, quickly manifests itself; whereas if such favourable climatic conditions had not been forthcoming, the fungus would have remained undeveloped in the haulm, and the crop matured free from disease. When slightly diseased tubers are grown for experimental purposes, and exposed to those conditions known to favour the appearance of the disease—dull light, excess of moisture in the air, and a fairly high temperature—special care being exercised to prevent external infection, the disease almost invariably appears; whereas if a second portion of the same tubers—used for the above experiment—are planted in the open air, and there is an absence of the exceptional climatic conditions indicated above, no outward trace of the disease may appear. However, if a few of the leaves from the apparently healthy plants grown in the open air are placed in damp air under a bell-jar in a dull light, within two or three days the leaves will show a copious development of potato blight, proving that the fungus was present in the tissues, and only awaiting those conditions favourable for its complete development.

Phytophthora has only one form of reproduction by means of spores, and these are produced only on the living leaves of the potato plant. Furthermore these are not resting-spores, but germinate the moment they are mature, and perish within a very short period of time unless they happen to be located on the leaf of a suitable host-plant. It is thus impossible for the European outbreak of potato disease to have originated from spores.

The disease must have come from the New World under the form of hybernating mycelium in the tuber, and by the same means it has unknowingly been sent from Europe to various other parts of the world.

At the present day *Phytophthora* has spread from the potato to some allied European wild plants, a fact to be borne in mind in connection with the possible means by which a crop may become infected.

As regards bulbs, *Chionodoxa luciliae*, a beautiful early spring-flowering bulbous plant, came to us from Asia Minor. Some time after its introduction a variety of this plant, described as differing in the possession of a 'black eye,' was imported. The 'black eye' proved to be due to the presence of a smut fungus (*Ustilago*) developed in the anthers. Further investigation showed that a perennial mycelium of this fungus was present in the 'cushion' or flattened stem from which the bulb-scales spring. This mycelium grows up inside the flower stem, and produces its spores in the anthers. The mycelium also passes from the parent bulb into the young bulbs to which it gives origin. Hence every bulb is infected, and in the majority of instances bears smutted anthers, but not always. Smutted plants have been under observation for the past ten years at Kew, and although in the majority of instances the anthers have been smutted, every now and again flowers free from smut have appeared, although examination of the bulb in such instances showed the presence of living mycelium.

Special stress is laid on the fact that tubers or bulbs proved to contain the germs of a disease do not necessarily *always* develop that disease in their offspring, because potato growers often discredit the statement that the potato disease can be transmitted through the tubers. Their argument is that on occasions healthy plants have grown from obviously diseased tubers that have been thrown on one side, and grown spontaneously. Undoubtedly so; a fungus, like every other plant, has its limitations, and under certain climatic conditions, favourable to the potato, and consequently unfavourable for the fungus, the latter would be unable to assert itself. Notwithstanding, it is not wise to plant potatoes or bulbs known to be diseased; the risk is great.

It is not necessary to remind those who have paid attention to the cultivation of bulbous plants, of the danger arising from the use of lily or snowdrop bulbs that have been previously attacked by the fungus called *Botrytis.*

Legislation has not dealt in any way with the source of danger indicated above, neither is it conceivable how it could do so. If attempted, to secure any prospect of success, potatoes would have to be cut into slices in search for specks of browning, and the cushion of each bulb would require to be examined microscopically. This statement, of course, does not apply to potatoes and bulbs only.

A third source of danger of introducing new diseases into distant countries is through the medium of living plants and ripe fruit.

In the case of fruit-trees, among the most destructive diseases are 'Apple-tree canker' (*Nectria ditissima*), which in its advanced stage is very conspicuous, but in its incipient condition on young trees, such as are exported, it is very doubtful whether its presence would be detected in a cursory examination at the port of entry. 'Apple-tree mildew' (*Sphaerotheca mali*) is very conspicuous on the foliage, but if the foliage is not present it would not be detected, but would certainly reveal itself when new leaves appeared, as the mycelium of this fungus hybernates in the branches.

Much has been made of the recent appearance of the American gooseberry mildew in Ireland. How was it introduced? No one knows, or, if they do know, do not appear to be inclined to tell. The point is, Was it introduced on living plants in its fully developed, conspicuous condition, in which case it could not have escaped the eye of an official on the lookout for diseases, or did it come under the form of spores adhering to the plant, which in due season produced the disease? In the latter case no official, however observant, could have detected its presence. To state that if legislation on the point had been in force the disease would not have entered Ireland, is only the expression of an enthusiast, and will not bear criticism.

Another very destructive disease that has found its way from one country to another is 'Peach leaf-curl' (*Exoascus deformans*). When the diseased foliage is present this disease is unmistakable, but after the foliage has fallen the tree shows no trace of its presence. Nevertheless the disease is present, as the mycelium is perennial in the branches, and would probably reveal itself the following season.

The importation of ripe fruit into a country is undeniably a source of danger. Many kinds of foreign fruit examined at Kew have furnished fungus spores which have germinated readily, and which, if they had found their way to the proper host-plant, would undoubtedly have established a disease. One redeeming feature in this case lies in the fact that the bulk of imported fruit is consumed in towns, consequently the spores are not so likely to reach those places where infection would result.

Two of the most injurious and most widely distributed diseases on ripe apples are 'Brown rot' (*Monilia fructigena*), and 'Apple scab' (*Fusicladium dendriticum*). It is very important to remember, however, that the spores from ripe fruit are not the sole means of propagating these diseases. Although fruit growers only recognise these as fruit diseases, as a matter of fact, in both instances, the disease first attacks the leaves, where its presence can only be detected by an expert. The spores formed on the leaves are washed by rain on to the young fruit, and in course of time the disease shows itself under the form of scab or brown rot.

It is obvious that in these instances scab and brown rot could be conveyed from one country to another quite as readily on living trees as on ripe fruit. Furthermore, trees conveying the disease need not necessarily bear leaves. If a tree has suffered from disease, spores of the fungus are washed by rain down the stem and branches, and remain in cracks in the bark until the following spring, when they germinate, and in many instances gain access to the leaves, and infection results.

It is mostly in connection with the importation of living plants and fruit that legislation has been called in as a safeguard, but, as will be seen from the above account, as at present carried out, that is, examination at the port of entry, it merely touches the fringe of the subject, and in the proper sense is but a very poor makeshift for securing immunity against the entrance of fungus diseases into a country.

To render legislation more effectual in the case of imported living plants, all such should, immediately on arrival, be submerged for five minutes in a tank containing a fungicide, the nature of which would depend on whether the trees were in a resting condition or bearing foliage. After this preliminary precaution the plants should be placed in quarantine for at least a year. That is, they should be planted in a certain place under the control of a specialist, whose duty would be to spray the plants *all over*, from time to time, more especially when in a resting condition, as at this period far more drastic measures can be applied with safety. By such means all superficial spores would be killed. If, on the other hand, an active disease showed itself, the plant should be promptly destroyed. It seems absolutely necessary that all these precautions should be taken before living plants, imported into a country, should be allowed to be sold and scattered broadcast through the country. If once distributed, the purchaser may not recognise a disease, or if he does, would not in all probability promptly destroy the tree, but hope for the best, until the disease became established and beyond control.

As to whether such methods will be followed remains to be seen; so far as the importation of ripe fruit, more especially apples and pears, into this country is concerned, there is nothing to fear; we are already well provided with all known diseases.

Finally, it is more than doubtful whether diseases are mainly introduced into a new country through the ordinary channels of trade. It is directly opposed to common experience, also to careful investigation, to conclude that diseased plants are sent out by nurserymen.

In these days of rapid transit numerous small packages containing seeds, which may have fungus spores adhering, or a few potatoes, which may possibly contain mycelium of the fungus causing potato blight or leaf-curl in their substance, are being constantly sent to friends residing abroad, and by such means diseases are disseminated in a way well outside practical legislation.

In discussing the spread of disease from an infected area to another adjoining area, or, in other words, from one part of a country to another, the subject has to be viewed from a different standpoint to that followed up to the present. New factors of importance have to be considered, as the dispersion of spores by wind, animals, insects, and perhaps most of all through human agency. The constant interchange of seed grown in different districts, etc., favours the dispersion of disease. These all lie outside the sphere of legislation, and unfortunately, it must be admitted, also often outside the sphere of preventive measures that can be applied by the practical man. It is in this connection that spraying is of real service in checking the spread of a disease, and if used in the sense of a preventive rather than as a cure, beneficial results will follow.

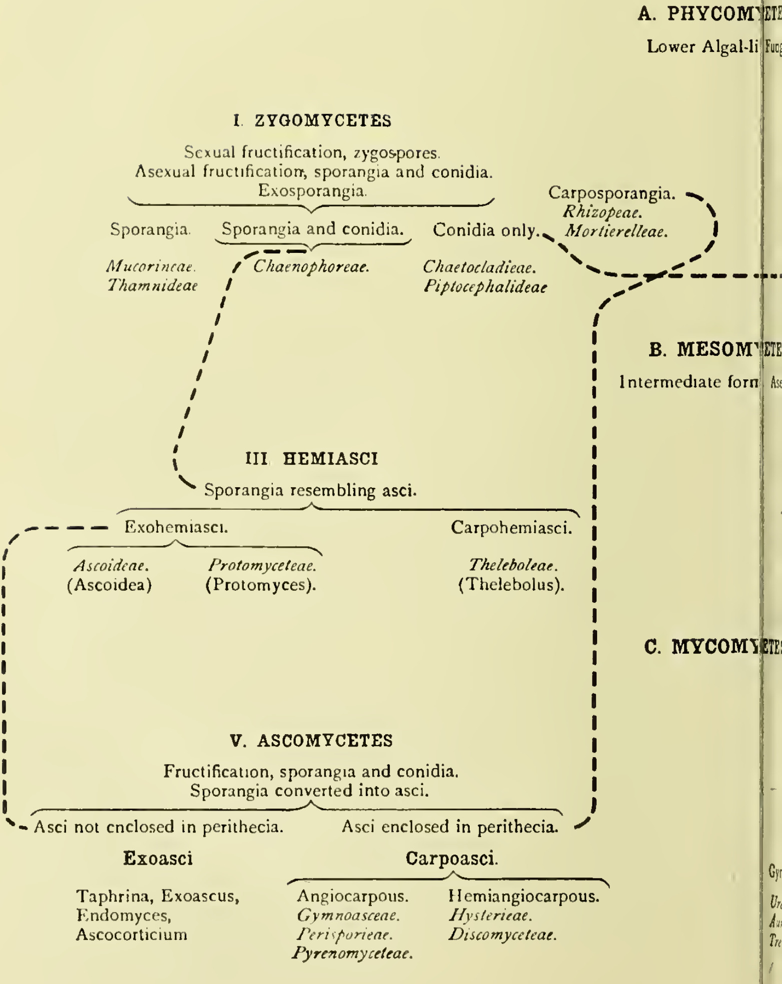
The only remaining point requiring notice, perhaps the most fruitful of all in disseminating disease to surrounding areas, is neglected gardens and orchards, which in this country are far too abundant. Such places become in time centres of disease, from which material for infection spreads in every direction. To suppress this possibility, the outcome of sheer neglect or thoughtlessness, drastic legislative measures are in force in some countries.

The above statements must not be interpreted as a tirade against legislation, but simply to indicate some of its weak points, as at present administered, and at the same time to prevent too bitter disappointment on the part of those who are inclined to expect through legislation, however strictly enforced, any marked decrease in the number or intensity of plant diseases caused by fungi.

Several definitely proved examples of modes of disseminating disease have been indicated which are obviously outside any possible legislative code that could be formulated. These, however, by no means exhaust the list of cases. The transportation of straw and forage is a wholesale means of diffusing diseases of cereals and grasses, as the spores of many of these fungi suffer no injury in even passing through the alimentary tract of an animal. Again, no law would insist on a man collecting and burning all diseased potatoes or turnips met with in a field, even if in a condition to be collected.

In some instances a plant that has been introduced to a new country has been attacked by an indigenous fungus. The coffee disease in Ceylon is a case in point. Soon after its introduction it was attacked by a fungus called *Hemileia vastatrix*, which resulted in the cessation of coffee cultivation in the island. From this centre the disease spread contemporaneously with the cultivation of coffee, and has practically rendered unremunerative this branch of industry throughout the old world.

BREFELD'S CLASSIFI



A. PHYCOM

Lower Algal-li

I. ZYGOMYCETES

Sexual fructification, zygospores.
Asexual fructification, sporangia and conidia.

Exosporangia.

- Sporangia.
  - *Mucorineae.*
  - *Thamnideae*
- Sporangia and conidia.
  - *Chaenophoreae.*
- Conidia only.
  - *Chaetocladieae.*
  - *Piptocephalideae*

Carposporangia.
Rhizopeae.
Mortierelleae.

B. MESOM

Intermediate form

III. HEMIASCI

Sporangia resembling asci.

- Exohemiasci.
  - *Ascoideae.* (Ascoidea)
  - *Protomyceteae.* (Protomyces).
- Carpohemiasci.
  - *Theleboleae.* (Thelebolus).

C. MYCOMY

V. ASCOMYCETES

Fructification, sporangia and conidia.
Sporangia converted into asci.

- Asci not enclosed in perithecia.
  - **Exoasci**
  - Taphrina, Exoascus, Endomyces, Ascocorticium
- Asci enclosed in perithecia.
  - **Carpoasci.**
  - Angiocarpous.
    - *Gymnoasceae.*
    - *Perisporieae.*
    - *Pyrenomyceteae.*
  - Hemiangiocarpous.
    - *Hysterieae.*
    - *Discomyceteae.*

ATION OF FUNGI

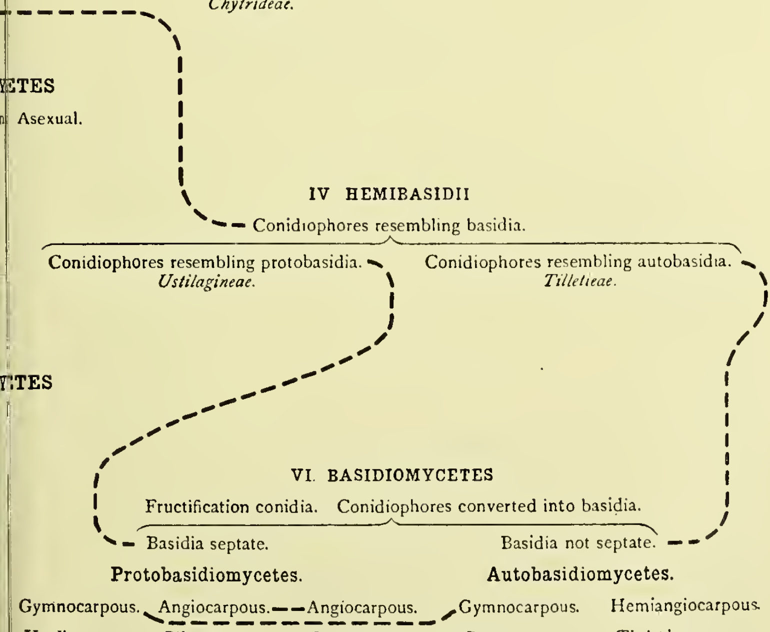
ETES

Fungi.

II. OOMYCETES

Sexual fructification, oospores.
Asexual fructification, sporangia and conidia.

Sporangia and conidia.	Conidia only.
Peronosporeae. *Saprolegnieae.* *Chytrideae.*	*Entomophthoreae.*



ETES

Asexual.

IV HEMIBASIDII

Conidiophores resembling basidia.

Conidiophores resembling protobasidia.	Conidiophores resembling autobasidia.
Ustilagineae.	*Tilletieae.*

TES

VI. BASIDIOMYCETES

Fructification conidia. Conidiophores converted into basidia.

Basidia septate.	Basidia not septate.
Protobasidiomycetes.	**Autobasidiomycetes.**

Gymnocarpous.	Angiocarpous.	Angiocarpous.	Gymnocarpous.	Hemiangiocarpous.
Uredineae. *Auricularieae.* *Tremellineae.*	*Pilacreae.*	*Lycoperdeae.* *Nidularieae.* *Phalloideae.* *Hymenogastreae.*	*Dacryomyceteae.* *Clavarieae.* *Tomentelleae.*	*Thelephoreae.* *Hydneae.* *Polyporeae.* *Agaricineae.*

The whole of this chapter, with the exception of the last paragraph relating to coffee disease, appeared in the

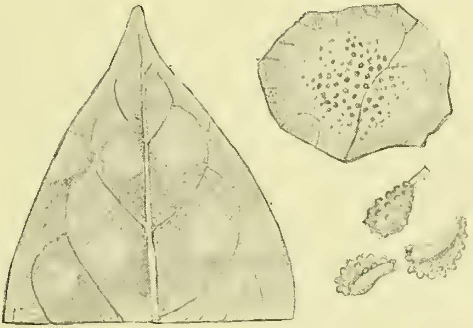


FIG. 56.—*Hemileia vastatrix*, a fungus belonging to the Uredineae, causing the destructive coffee disease. 1, portion of a coffee leaf showing diseased patches, which are bright orange in colour; 2, a diseased patch, slightly enlarged, showing a sorus or group of uredospores; 3, uredospores, highly mag.

Gardeners' Chronicle, Dec. 23 and 30, 1905, and Jan. 6, 1906.

III. CLASSIFICATION

PRIMARY GROUPS OF FUNGI

The three primary groups of fungi—Phycomycetes, Ascomycetes, and Basidiomycetes—established long ago from a purely morphological standpoint, still stand unassailed; in fact, the problem mostly exercising the minds of cytologists is the relationship of these groups to each other. By almost common consent the starting-point of the fungi is represented by the Phycomycetes; afterwards sequence of origin and relationship is mostly a matter of personal opinion.

Among modern schemes of classification comprising the whole of the fungi may be mentioned that of Saccardo, as evolved in his *Sylloge Fungorum*. This is said to be a carpological system, based on the features derived from the sporocarp, but it might more accurately have been defined as a sporological system, as the leading features characterising minor groups, genera, and species turn almost exclusively on characters presented by the spores; such characters depending on the colour and presence or absence of septa. This applies to the Ascomycetes and the Basidiomycetes. In the Phycomycetes no new ideas are presented. This system, based entirely on characters presented by mature plants, cannot necessarily indicate true affinities, but only features of morphological agreement, which in many instances are obviously only coincidences or analogies ; but Saccardo did not start with the intention of indicating homologies; his object was to enable a person to determine the name by which a fungus is known, and thus furnish a fixed starting-point for the research student. In this respect Saccardo has succeeded, so far as the material at his command admitted.

The fungi in Engler and Prantl's *Pflanzenfamilien* are not yet completed. Different authors are responsible for the various groups, and as each author appears to have followed his own ideas, there is a lack of continuity in the scheme of classification as compared with Saccardo ; nevertheless the work, so far as completed, is a valuable addition to our knowledge of the fungi, and the numerous illustrations and references to literature far exceed those of any previous work on the subject.

The classification of fungi presented by Brefeld, the outcome of many years of careful study, as evidenced by his published work, was presented as indicating the true sequence and affinities of the respective groups of fungi. In this particular we now know that he has to some extent failed. But, viewed impartially, it must be admitted that the leading idea running through Brefeld's work, and his main arguments, are based on morphological evidence, and the results of cultures. There is no internal evidence to show that Brefeld ever attempted that line of investigation which alone can enable a person to pronounce with certainty the absence or presence of sexual reproduction in a given group. Brefeld's contention that sexuality, in a potential form, is entirely confined to the Phycomycetes suggests a preconceived view, which, without further evidence, was adhered to.

A careful examination of Brefeld's latest arrangement of the origin and sequence of the larger groups, here reproduced, will, I think, support this view.

The Phycomycetes, or lower, algal-like fungi, are divided into two main groups, the Zygomycetes, whose sexual reproduction results in zygospores. In the Oomycetes the result of sexual reproduction is an oospore. Zygospores and oospores do not play any part in the further evolution of fungi, all later groups being derived from the asexual forms of reproduction present in the Phycomycetes, which are respectively sporangia and conidia, and rests entirely on morphological resemblances.

It will be further observed that the Oomycetes play no part in the scheme of evolution, all succeeding groups being derived from the Zygomycetes.

Choenophoreae, a family of the Zygomycetes possessing both sporangia and conidia, gives origin to the Hemiasci. The latter are divided into two groups: Exohemiasci, without any trace of a perithecium, and the Carpohemiasci, having the first rudiment of a perithecium or protective covering enclosing the hemiascus. This last feature is inherited from the Carposporangia group of the Zygomycetes. The important character of the Hemiasci consists in the variable number of spores contained in the ascus-like sporangium. The Ascomycetes are derived from the Hemiasci, and are characterised by the ascus containing a definite number of spores. The Exoasci are derived from the Exohemiasci, and the Carpoasci from the Carpohemiasci. Chaetocladieae is a family considered by Brefeld to possess conidia only as its asexual form of fruit. Most other mycologists consider Brefeld's conidia as sporangia. These structures differ from ordinary sporangia in containing only one spore instead of a large number. From this family alone Brefeld derives the Hemibasidii. This group consists of two main sections, the Ustilagineae, having a promycelium divided into three or four cells by cross-walls; each cell gives origin to several sporidia or secondary spores. The second group, Tilletiae, has an aseptate promycelium which bears a variable number of secondary spores at its apex. The Basidiomycetes are derived directly from the Hemibasidii, and again are divided into two principal groups. Protobasidiomycetes come from the Ustilagineae, and differ from the latter in each cell of the promycelium bearing one sporidium only. This difference raises a promycelium to the rank of a basidium, and the secondary spore or sporidium to the rank of a spore proper. The second group composing the Basidiomycetes, the Autobasidiomycetes, is derived from the Tilletiae, and, like the latter, has the basidium aseptate or one-celled, and bearing a definite number of spores at its apex, usually four. It will be observed that the one point of difference between the Hemibasidii and the Basidiomycetes consists in the promycelium in the first-named group bearing a variable number of secondary spores or sporidia, whereas in the last-named group the promycelium (now a basidium) bears a definite number of sporidia (now termed spores).

The above brief review of Brefeld's scheme of classification indicates very clearly that, from his point of view, morphological features are alone of value in indicating descent, and that if the sexuality theory was eliminated, his system would not be in any way interfered with.

This arrangement of the larger groups is, I consider, the most satisfactory, from a morphological standpoint, that has up to the present been submitted, and, with minor modifications, will be adopted in the systematic portion of this work.

The most important departure from Brefeld's scheme consists in the inclusion in the Hemiasci of all families having the perithecium absent or comparatively rudimentary, as Gymnoasceae, the genera *Exoascus*, *Taphrina*, etc. *Thelebolus* returns to the Discomycetes, in the family Ascobolaceae; the reason for this change has already been given. Consequently Brefeld's Carpohemiasci section of the Hemiasci, based entirely on the genus *Thelebolus*, ceases to exist.

Brefeld, *Unters. d. Mykol.*, Heft 1-13 (1872-1905).

Engler and Prantl, *Pflanzenfamilien*, 1, 1; 1, 1** (1897-1900).

Saccardo, *Sylloge Fungorum*, 1-18 (1882-1905).

SERIAL ARRANGEMENT OF THE FUNGI FOLLOWED IN THIS BOOK

Sub-Kingdom. **FUNGI.**

Order.	**Phycomycetes.**
Family.	Chytrideae.
,,	Protomycetae.
,,	Mucorineae.
,,	Entomophthoreae.
,,	Peronosporeae.
,,	Saprolegnieae.
Order.	**Hemiascomycetes.**
Family.	Gymnoasceae.
,,	Exoasceae.
,,	Saccharomycetae.
Order.	**Ascomycetes.**
Sub-Order	**Pyrenomycetes.**
Family.	Perisporieae.
,,	Sphaerieae.
,,	Hypocreae.
,,	Dothidieae.
,,	Microthyrieae.
,,	Lophiostomeae.
,,	Hysterieae.
,,	Tuberaceae.
,,	Phymatosphaerieae.
Sub-Order.	**Discomycetes.**

Family.	Cyttarieae.
,,	Helvelleae.
,,	Pezizeae.
,,	Ascoboleae.
,,	Dermateae.
,,	Bulgarieae.
,,	Sticteae.
,,	Phacideae.
,,	Patellarieae.
,,	Cordieriteae.
Sub-Order.	**Laboulbeniaceae.**
Family.	Peyritschielleae.
,,	Laboulbenieae.
,,	Zodiomycetae.
Order.	**Hemibasidiomycetes.**
Family.	Ustilagineae.
,,	Auricularieae.
,,	Uredineae.
,,	Pilacreae.
,,	Sirobasideae.
,,	Tremelleae.
,,	Hyalorieae.
Order.	**Basidiomycetes.**
Sub-Order.	**Hymenomycetes.**
Family.	Dacryomyceteae.
,,	Clavarieae.
,,	Thelephoreae.
,,	Hydneae.
,,	Agaricineae.
,,	Polyporeae.
Sub-Order.	**Gasteromycetes.**
Family.	Hymenogastereae.

Family.	Sclerodermeae.
,,	Nidularieae.
,,	Lycoperdeae,
,,	Phalloideae.
Order.	**Deuteromycetes.**
Sub-Order.	**Sphaeropsidiaceae.**
Family.	Sphaeroideae.
,,	Nectrioideae.
,,	Leptostromeae.
,,	Excipuleae.
Sub-Order.	**Melanconieae.**
Family.	Melanconieae.
Sub-Order.	**Hyphomycetes.**
Family.	Mucedineae.
,,	Dematieae.
,,	Stilbeae.
,,	Tubercularieae.

FUNGI

In our present state of knowledge, it is impossible to give a concise definition that shall include all fungi, and at the same time exclude all other forms of plant life. Negative characters perhaps afford the clearest conception of the group, as contrasted with other plants.

The absence of chlorophyll and consequent necessity for organic food, coupled with the absence of true parenchymatous tissue, which is replaced by more or less compacted strands of cells or hyphae not organically joined laterally, constitute the most pronounced characteristics. It is important to bear in mind that the two features indicated must be in combination to constitute a fungus, as both characters are not uncommon in other groups of plants.

In seed-bearing plants the absence of chlorophyll is not uncommon, but systems of tissue are present. On the other hand, in many of the lower algae the plant consists of a filament composed of a single row of cells, in fact structurally a hypha, but chlorophyll is present.

KEY TO THE ORDERS

Aquatic, or inhabiting damp localities. Mostly minute, vegetative hyphae often continuous, and not interwoven to form compact tissues. Products of sexual reproduction, zygospores or oospores. Asexual reproduction by conidia, which often liberate motile zoospores. *Phycomycetes.*

Parasitic or saprophytic. Mostly minute fungi either having a variable number of spores in an ascus, or the asci are naked (not enclosed in a perithecium), or the perithecium is rudimentary. *Hemiascomycetes.*

Parasitic or saprophytic. Aerial, minute or large, sometimes perennial. Asci containing a definite number of spores, usually eight. Perithecium always present. *Ascomycetes.*

Obligate parasites. Promycelium of germinating spore short, either divided into 3-4 cells by septa, and each cell bearing one or several secondary spores; or promycelium not septate and bearing a variable number of secondary spores at its apex. *Hemibasidiomycetes.*

Saprophytes or parasites. Spores borne on basidia in definite numbers, most frequently four, basidia either one-celled, or transversely or cruciately septate. *Basidiomycetes.*

A heterogeneous assemblage of minute fungi producing conidia only, produced either in perithecia or on naked conidiophores. Some have been proved to be conidial forms of the higher fungi, and the remainder are suspected to belong to the same category. *Deuteromycetes.*

PHYCOMYCETES

In most systematic works a fundamental characteristic of the present order is said to be the absence of transverse walls or septa in the hyphae. How this misconception could arise in the first place is difficult to understand, and why it is continued in quite recent works passeth all understanding. Perhaps the statement is intended to apply to the primitive or the sexual phase only. In *Protomyces*, a very simple type, the hyphae are very distinctly septate. The same is true of *Dispyra*, and Thaxter has pointed out their presence in *Dimargaris*. Septa are often abundant in the vegetative hyphae of *Mucor*, etc., and when we come to the conidiophores of aerial forms, septa are very frequently present. The instances given do not apply to the formation of septa just prior to the development of antheridia, oogonia, chlamydospores, etc.

On the other hand, many species are aseptate until the organs of reproduction are formed, agreeing in this respect with *Vaucheria*, and some other algae.

In the family Apodyeae of Fischer true septa are absent, but there is a characteristic segmentation of the hyphae indicated by constrictions due to the deposit of a substance called cellulin, which nearly closes the lumen of the hypha at the point of constriction, only a small central pore remaining open, through which the protoplasm passes.

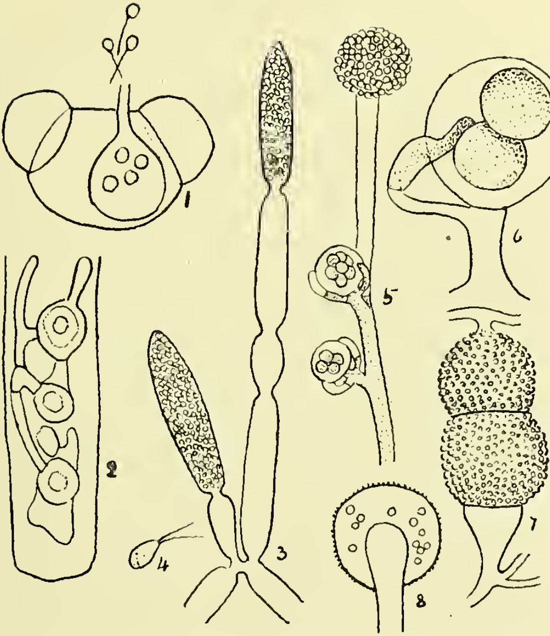


FIG. 57.—1, *Olpidium pendulum*, immersed in a pollen grain of a conifer, the swarmsporangium liberating one-ciliate swarmspores or zoospores (after Braun); 2, *Lagendium Rabenhortsii*, producing oospores, growing in the filament of a fresh-water alga (after Zopf); 3, *Leptomitus lacteus*, the terminal portions transformed into zoosporangia; 4, biciliate zoospores of *L. lacteus*; 5, *Achlya racemosa*, the terminal cell a zoosporangium liberating zoospores which form a compact ball at the mouth of the zoosporangium; lower down on the branch are oospores with antheridia; 6, *A. racemosa*, oogonium containing two oospheres: an antheridium is penetrating the oogonium (after De Bary); 7, zygospore of *Mucor stolonifer*: the upper cell is a large suspensor and should be smooth, not warted, as shown by mistake: the suspensors vary much in size; 8, *Mucor mucedo*, sporangium seen in optical section, showing columella and a few contained spores. All highly mag.

Leptomitus lacteus, a species not uncommon in ditches and rivers, more especially where organic matter is emptied from manufactories, etc., illustrates this structure. This feature also has it counterpart in algae.

In some genera belonging to Chytridieae, as *Rozella* and *Reessia*, the protoplasm during the vegetative condition is not enclosed by a cell-wall, but remains naked and amoeboid in the cells of the host.

Klebs, in studying *Saprolegnia mixta*, came to the conclusion that gemmae are of no value from a phylogenetic point of view. They are special structures, whose use is to tide over periods when the formation of other spores is precluded. They behave like ordinary hyphae, and give origin to oogonia or sporangia depending on environment.

The special structures that give origin to zoospores are called zoosporangia.

All the species are minute, and come under the category of microscopic fungi; some species consist of a single cell, entirely destitute of mycelium.

A considerable number are parasitic on plants or animals, as *Phytophthora infestans*, causing the too well-known potato disease, and *Saprolegnia ferox*, the origin of the equally destructive salmon disease.

Many species are truly aquatic, and have spores possessed of voluntary movement, hence called zoospores. The great majority of fungi that have adapted themselves to aerial conditions have ceased to produce zoospores, non-motile spores, diffused by wind, insects, birds, and other agents, having taken their place. The fungus causing potato disease, *Phytophthora infestans*, is an illustration of a connecting link between the primitive aquatic fungi and their modern aerial descendants. Although this fungus has adapted itself in some respects to aerial conditions, yet its only reproductive bodies known consist of the aquatic type of motile spores or zoospores. So long as fungi remained aquatic, motile spores were a decided advantage; their power of spontaneous movement enabled them to come in contact with new hosts. On dry land the advantage of spontaneous movement is not obvious, in fact it retards the diffusion of the spores, and infection can only be secured when the host-plant is covered with moisture. To compensate for this shortcoming, a vegetative method of continuing the species has been evolved. When a potato plant is infected, some of the mycelium of the fungus passes into the tubers; there it remains in a resting condition, its presence being indicated by rusty patches in the flesh. When a tuber thus infected is planted, the mycelium grows up along with the stems of the potato, and finally passes into the leaves, where, if climatic conditions are favourable, it produces fruit. Some of the mycelium again passes into the young tubers. By means of this vegetative method of reproduction, the disease can pass from one generation of potatoes to another without the intervention of spores. Many other kinds of fungi also depend much on the presence of persistent mycelium in the tissues of the host-plant for their periodical appearance; in fact some species, as the fungus present in the grain of *Lolium temulentum*, have so perfected this vegetative mode of reproduction, that the production of spores has been entirely arrested.

Future investigation will probably show that the presence of hybernating mycelium has much more to do with the occurrence of fungus epidemics than is at present suspected.

Distribution cosmopolitan.

Klebs, *Pringshm. Jahrb.*, 33, p. 573 (1899).
Thaxter, *Bot. Gaz.*, 20, p. 517.

KEY TO THE FAMILIES

I. Hyphae rudimentary or obsolete.

A. **Archimycetes**

Sexual reproduction by zygospores; asexual by zoospores. Aquatic and endoparasitic in algae, fungi, and infusoria, or aerial and endoparasites in plants. *Chytridieae.*

Sexual reproduction only known; sporangia thick-walled, eventually producing zoospores. Aerial and endoparasitic in plants. *Protomyceteae.*

II. Hyphae well developed.

B. **Zygomycetes**

Sexual reproduction by conjugation of gametes, forming a zygospore.

Asexual reproduction by spores formed in sporangia. Chlamydospores are also formed by some species. Aerial saprophytes. *Mucorineae.*

Asexual reproduction by free conidia borne on hyphae; also by thick-walled asexual resting-spores. Attacking living insects and producing conidia after the hosts' death. Rarely parasitic or saprophytic on plants. *Entomophthoreae.*

C. **Oomycetes**

Sexual reproduction by antheridia and oogonia, forming oospores.

Asexual reproduction by conidia usually borne on much-

branched conidiophores. On germination the conidia either emit a germ-tube or liberate zoospores. Aerial; endoparasitic on living plants, mostly on leaves.
Peronosporeae.

Asexual reproduction by zoospores. Aquatic fungi parasitic on fishes, insects, and plants. *Saprolegnieae.*

Chytridieae

The most primitive forms of fungi at present known, almost or entirely destitute of mycelium, and in many respects closely approaching some of the lowest forms of animal life, from which Dangeard suggests the fungi have descended through such forms as *Polyphagus*, etc.

Either aerial and parasitic in the tissues of plants, or aquatic and parasitic on fresh-water algae, fungi, or infusoria.

Many of the so-called species are imperfectly known; one, however, described in detail by Nowakowski, is summarised as follows by De Bary:—

'*Polyphagus euglenae*, a parasite upon resting *Euglena viridis*, has become the best known of the Chytrideae through Nowakowski's beautiful investigations. The swarmspore [zoospore], when it has come to rest in the water, becomes spherical in shape, and at once puts out hair-like, tubular rhizoid processes in indefinite directions. If one of these encounters a resting *Euglena* it penetrates into its body, destroying and exhausting it to supply food to the parasite. The parasite then begins to increase in size, the rhizoid tubes become larger and thicker, and new ones are formed which throw out branches, and attack and destroy any new Euglenae which they encounter. In this way a much-branched plant is formed with hair-like terminal branchlets, which connect with the larger main stems, and through these with the body of the original spore; the latter has grown in the meantime into a large, round, or elongated vesicle at the expense of the Euglenae, which

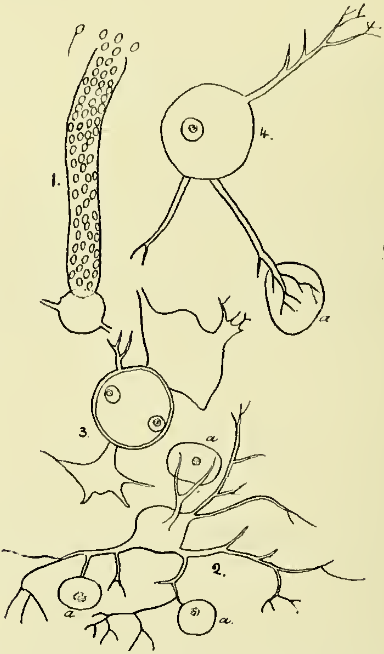


FIG. 58.—*Polyphagus euglenae.* 1, a zoosporangium liberating one-ciliate swarmspores; 2, a *Polyphagus* attacking *Euglenae*, *a*, *a*, *a*; 3, zygospore of *Polyphagus* containing two nuclei; 4, cyst of *Polyphagus*, containing one nucleus. (Figs 1-2 after Nowakowski; figs 3-4 after Dangeard.) All highly mag.

have been exhausted by the rhizoids. When it has reached a certain size, varying according to the food which has been supplied to it, it shows itself in many specimens to be a sporangium, or, if the term is preferred, a *prosporangium*. It grows out at one spot into a bluntly and irregularly cylindrical, thick tube, with a delicate membrane, into which the whole of the protoplasm passes, and is at once divided into swarmspores. This process of development may be repeated for many generations, and leads to an immense multiplication of individuals, if there is a sufficient number of Euglenae within reach. When this has taken place, the course of events changes. The young plants remain for the most part small, and become gametes which conjugate in pairs, each pair forming a zygospore, and these behave as resting-spores. The two conjugating gametes of a pair have no definite position or distance with respect to one another, and are similar in form to the non-conjugating plants. The one which from the processes to be described may be termed the supplying gamete (abgebende gamete) [male organ] has usually a round and larger body, but shows no other apparent difference before contact with the other, the receptive gamete (aufnehmende gamete) [female organ]. The latter usually continues to be smaller, and often very small, and puts out rhizoid branches, and if one of these, after longer or shorter growth, encounters a supplying [male] gamete, it applies its extremity to it as a conjugating tube, and increases in thickness, while it ceases to grow in length. The membrane between the conjugating tube and the supplying gamete disappears at the point of attachment, and an open communication between them being thus established, the whole of the united protoplasm of both gametes passes into an enlargement of the conjugation tube, close to the point of attachment; the swelling gradually expands into a spherical vesicle, and, being delimited by a membrane after receiving the protoplasm, becomes a thick-walled zygospore. The outer wall of the zygospore assumes a pale yellow colour, and in some cases continues smooth, in others is covered with short spikes, which begin to form at the same time as the enlargement in the tube. The whole process of forming a zygospore, from the attachment of the conjugating tube and the maturation of the zygospore, was completed, in the case observed by Nowakowski, in about 6-7 hours. A few instances are known of the conjugation of 2-3 receptive with one supplying gamete, and of the consequent formation of 2-3 zygospores. The zygospore, as has already been said, is a resting-spore. It germinates when its resting time is over, and produces a zoosporangium like the non-conjugating plants.'

Dangeard, who has recently studied the structure and mode of sexual reproduction of *Polyphagus euglenae*, has added materially to the above observations, which were conducted from a morphological standpoint only. This author announces the important fact that the female gamete contains only one nucleus, the male gamete also contains one nucleus; these meet in the zygospore, but remain indifferent to each other during the resting period, and only coalesce at the moment of germination. The same observer recorded for the first time the presence of what he terms cysts, apparently the equivalent of azygospores. These bodies are enclosed in a thick wall, and enter on a resting-stage like zygospores, but are not the outcome of conjugation. These cysts are said to be ordinary cells, which, under certain unknown conditions, enter a resting-stage and become clothed with a thick wall. Such cysts are distinguished from zygospores by the presence of well-developed, absorbing filaments, the homogeneous (not stratified) structure of the cell-wall, the absence of a large oil-globule in the centre of the cell, and by the existence of only one large nucleus, whereas zygopores contain two nuclei.

Protomyceteae

The mycelium is intracellular, vaguely branched, septate, producing numerous intercalary spores, after which it disappears. Sporangia and zoospores unknown. Resting-spores globose or broadly elliptical; wall thick, consisting of two or three layers. On germination the thin endospore protrudes through a rupture in the thick wall of the resting-spore as a sporangium, containing numerous minute, cylindrical, motionless spores that conjugate in pairs. After conjugation the spore emits a slender germ-tube which enters the tissues of the host, where it forms a mycelium which in turn produces resting-spores.

The masses of resting-spores often form hard, warty projections on the host-plant. Parasitic in the subepidermal tissues of flowering plants.

There is a difference of opinion as to the relative value of the present family. Its only genus, *Protomyces*, is reduced to subgeneric rank, being included in *Cladochytrium* by Fischer. Brefeld includes *Protomyces* in the Hemiascomycetes.

Mucorineae

The species are saprophytic, growing on decaying animal or vegetable substances, ripe fruit, dung, etc. In some species the sporangiophores are simple and bear a single sporangium at the tip, in others the sporangiophore is more or less branched, and in some cases bears sporangia of two distinct sizes and differing in other respects. Sexual reproduction by the conjugation of two gametes, which are sometimes of unequal size. Zygospores produced in the substance of, or on the surface of, the matrix.

KEY TO THE SUB-FAMILIES

A. Columella present. Mycelium stout, not anastomosing.

* Sporangium polysporous.

Wall of sporangium heterogeneous, upper portion cuticularised and persistent, basal zone deliquescent at maturity. *Piloboleae.*

Wall of sporangium homogeneous. *Mucorineae.*

** Sporangium monosporous. *Chaetocladieae.*

B. Columella absent. Mycelium slender and anastomosing.

Sporangium globose. *Mortierelleae.*

Sporangium cylindrical. *Syncephalideae.*

Piloboleae

These fungi grow on dung, and superficially resemble species of *Mucor*, from which *Pilobolus* is at once recognised by the much-swollen apex of the sporophore, which is usually beaded with drops of moisture. The swollen apex of the sporophore or elongated stem is an arrangement for suddenly projecting the small black sporangium to a distance when mature. Many of these sporangia

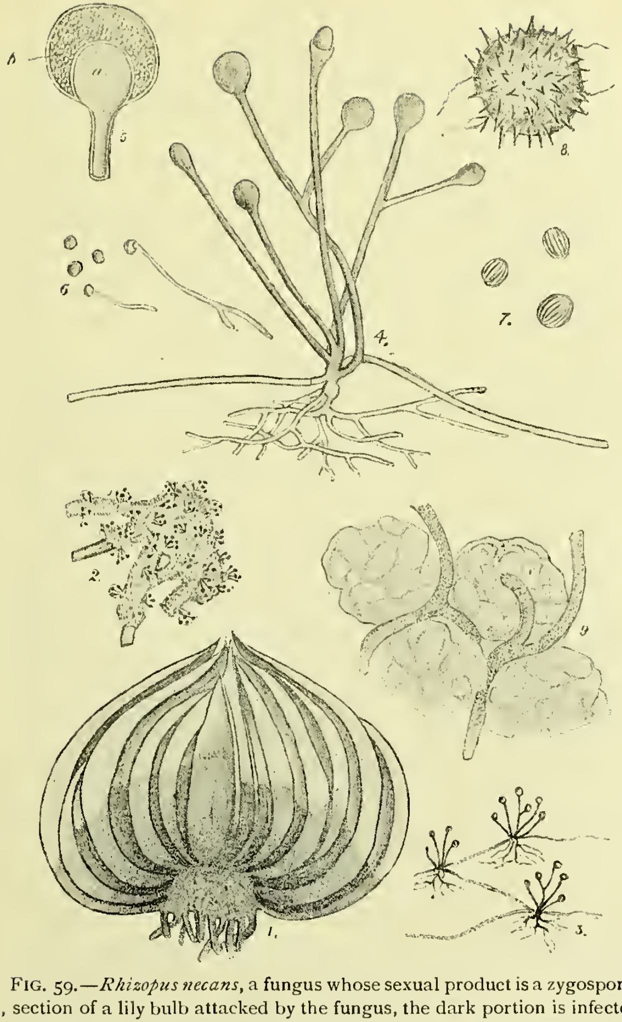


FIG. 59.—*Rhizopus necans*, a fungus whose sexual product is a zygospore. 1, section of a lily bulb attacked by the fungus, the dark portion is infected by the parasite ; 2, the fungus-bearing conidial fruit, and showing the habit of growth ; 3, conidial fruit on a larger scale ; 4, a single cluster of conidial fruit or sporangia, showing the rhizoids or vegetative hyphae at the base ;

[*Description continued on* p. 252.

replete with spores alight on growing grass surrounding the dung, and become fixed there by a viscid substance that is insoluble in water after it has been exposed to the air. If grass bearing such sporangia is eaten by some herbivorous animal, the spores pass uninjured through the alimentary canal, and produce a crop of the fungus on the dung. By this method the fungus is distributed, and it may probably be thus introduced to new countries on hay.

Mucorineae

Mycelium not anastomosing; sporangia polysporous, furnished with a columella and a homogeneous wall. Some species, as *Mucor*, form a copious vegetative mycelium, which spreads in the substratum. In other forms, as *Rhizopus* and *Circinella*, the vegetative mycelium is scanty. Characters of systematic importance are afforded by the sexual branches, which may be curved or straight, smooth or spinulose, etc. In some genera, as *Mucor*, *Phycomyces*, *Spinellus*, and *Sporodinia*, the progametes are of equal size, whereas in *Helicostylum*, *Thamnidium*, *Rhizopus*, and *Circinella*, the two progametes are unequal in size. In many species zygospores are rare, and in not a few forms, altogether unknown. In *Circinella* the branches bearing the sporangia are strongly recurved, and the sporangia dehisce in a circumscissile manner at the centre, the basal half persisting.

Many species are parasitic on decaying vegetable or

5, optical section of a sporangium: *a*, columella: *b*, sporangial sac filled with spores (technically conidia); 6, spores from sporangium, some germinating; 7, spores on a larger scale to show markings on epispore; 8, mature zygospore, the suspensors are indicated; 9, mycelium running between cells of bulb containing starch. Figs. 1 and 2, nat. size; rest mag.

animal matter, dung, etc.; some are incipient parasites on ripe fruit, etc., whereas some species of *Rhizopus* are destructive parasites.

Chaetocladieae

Growing on dung. Distinguished by the much-branched sporophore; all the main and secondary branches are sterile and end in spine-like points. Sporangia small, globose, usually warted, containing only one spore, springing in small clusters from short, lateral, ternary branchlets.

Chaetocladium Jonesii and *C. Brefeldii*, both British species, are not uncommon on dung, often mixed with *Mucor mucedo*, on which they are considered to be parasitic.

Mortierelleae

Mycelium slender, dichotomously branched and frequently anastomosing. Sporangiophores erect, often produced in small clusters, swollen at the base and tapering upwards, simple or branched, each branch terminated by a globose, polysporous sporangium without a columella.

In *Mortierella*, the only British genus, the branches of the sporophore are often arranged in a verticillate or corymbose manner.

Growing on decaying organic substances, fungi, wood, dung, etc.

Syncephalideae

Growing on dung, decaying organic substances, etc. Distinguished at once by the numerous cylindrical or slightly clavate sporangia springing from a swollen head, borne at the tip of an elongated stem.

Each sporangium containing a single row of spores, or in the clavate sporangia containing more than one row of spores at the apex.

Entomophthoreae

A characteristic feature of the present family is the production of a quantity of stout hyphae with oily or fatty contents. Many of the species are developed on insects, of which the best known is *Empusa muscae*, the one attacking the common house-fly, which becomes attached to a window-pane, and is soon surrounded by a white cloud of liberated conidia.

Asexual reproduction is effected by large, colourless conidia, which are elastically projected into the air at maturity. Sexual reproduction, by the conjugation of gametes, often of unequal size, and originating as lateral outgrowths of two distinct hyphae, as occurs in *Spirogyra* amongst the algae. The resulting zygospore, enclosed in a very thick, hard wall, becomes a resting-spore. Azygospores, similar in appearance to zygospores, and acting as resting-spores, are also formed by some species.

The members of the present family somewhat resemble the Saprolegnieae in habit, but are quite distinct in the mode of formation of the sexually produced resting-spores, and in the conidia not being motile.

Most of the species are entomogenous or parasitic on insects, but a few forms are met with on fungi, in the prothallia of ferns, or on the dung of frogs, lizards, etc.

Those that attack insects often attach the host firmly to some substance by means of specialised hyphae or rhizoids, the tips of which are often discoid. In other cases the insect is firmly fixed by its proboscis to the

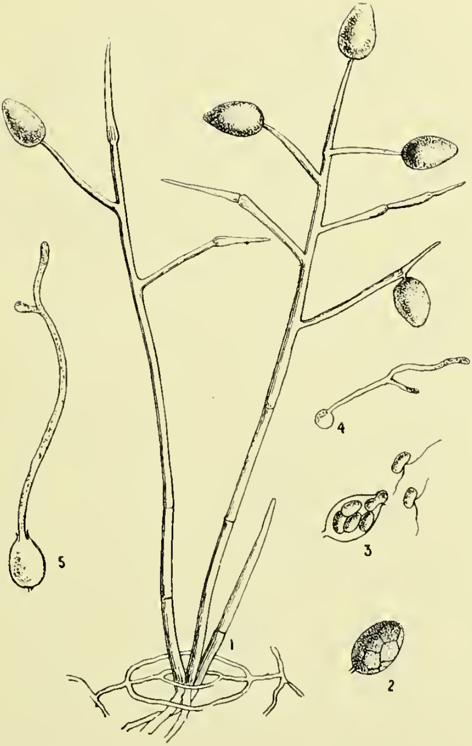


FIG. 60.—*Phytophthora infestans*, a fungus whose asexual reproductive bodies are usually motile zoospores. The sexual mode of reproduction has disappeared. In allied species the conidia do not contain zoospores, but produce a germ-tube on germination. This sometimes happens with ***P.** infestans*, which thus illustrates a fungus occupying a transitional stage between the older aquatic types which constantly produces zoospores, and the more modern types, where the conidia are dispersed by wind, and on germination produce a germ-tube.

substratum. Although in some instances the fungus would appear to produce little or no injury to the insect host, yet in most cases death is the outcome of the parasitism. In many instances the mortality to forms of insect life caused by members of the Entomophthoreae is very great and widespread, and as such mortality occurs amongst insects destructive to plants or animals, a correct knowledge of the life-history of this group of fungi becomes important from an economic standpoint.

Thaxter, an American mycologist, who has paid special attention to this group of fungi, describes an epidemic caused by these fungi as follows :—

'I have observed two epidemics caused by this species [*Empusa* (*Entomophthora*) *sphaerosperma*], one among certain small flies in a wood near marshy ground at Kittery, Me., where the hosts occurred in considerable numbers, fixed by the fungus on the under side of the lower leaves, a few feet from the ground. The second instance occurred in two orchards in the same locality, where the hundreds of the previously mentioned epidemic were replaced by tens of thousands, the host in this instance being the leaf-hopper (*Typhlocyba mali* and *rosae*), a pest only too well known to cultivators of roses. Having first observed it in some abundance on roses in a garden, I was led to make an examination of adjacent apple orchards, and found the lower branches of the trees literally covered with the affected hosts, a dozen or more being often fastened to a single leaf.'

The same author also describes *Entomophthora aphidis* as producing a similar wholesale destruction of the aphis so injurious to the hop plant.

Distribution general.

FIG. 61.—*Peronospora viticola*, a destructive parasite attacking the vine, and known as vine mildew. 1, under surface of vine leaf, showing patches of white mildew; 2, a group of conidiophores, emerging through a stoma of the leaf; 3, the conidia more highly mag.; 4, conidia liberating zoospores; 5, mature oospore or resting-spore, formed in the tissue of the leaf; 6, an oospore germinating, and producing a conidiophore; 7, autumnal form of conidiophore with a very short stem, and bearing only few conidia. Fig. 1, reduced; the remainder highly mag.

Peronosporeae

All the species are minute and parasitic, occurring mostly on leaves or young fruit, where they form a very delicate white or greyish felt. This felt consists entirely of conidiophores, which originate from mycelium in the interior of the host, and emerge through the stomata, or rupture the epidermis for the purpose of forming conidia in the air, where they are quickly dispersed. The conidia either produce zoospores, and are then in reality zoosporangia, or emit germ-tubes. Sexual reproduction by antheridia and oogonia ; the resulting oospores are formed in the substance of the matrix.

In the genus *Cystopus*, or *Albugo*, as it is now sometimes called, the conidia are produced in long chains ; in other genera they are solitary.

This family includes some of the most destructive parasites known, among which are included the vine mildew, *Peronospora viticola* ; the crucifer mildew, *P. parasitica* ; and last, but perhaps most destructive of all, *Phytophthora infestans*, the cause of the dreaded potato disease.

Saprolegnieae

Asexual reproduction by zoospores which are generally biciliate. In *Saprolegnia* and *Pythium* the zoospores are always destitute of a membrane ; in *Dictyuchus* and *Diplanes*, the zoospores at first have a distinct membrane from which they escape before leaving the zoosporangium ; whereas in *Achlya* and *Aphanomyces* the zoospores are naked while in the zoosporangium, and become invested with a membrane after their escape. The hyphae become partly or in some species entirely transformed into zoosporangia. Sexual reproduction by oogonia and antheria; in *Saprolegnia* the oogonium contains several oospores; in

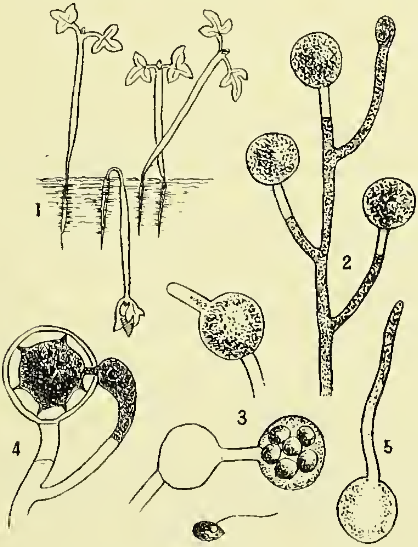


FIG. 62.—*Pythium debaryanum*, a parasite destructive to seedlings, and causing the disease known as 'damping off.' 1, seedlings of cress (*Lepidium*) attacked by the fungus; 2, mycelium bearing conidia at the tips of the branches; 3, sporangia in different stages, also a free zoospore; 4, an oosphere with the antheridium or male organ attached, which has pierced the wall of the oosphere and inserted a slender tube, for the purpose of allowing the contents of the antheridium to mingle with those of the oosphere (after this blending of contents, or fertilisation, the oosphere becomes enclosed in a newly formed cell-wall, to form the oospore or sexually produced resting-spore); 5, a germinating conidium. Fig. 1, nat. size; the remainder highly mag.

Pythium it is monosporous. In *Dictyuchus* the wall of the oogonium is perforated. Most of the species are truly aquatic, growing on fish, insects, or aquatic plants.

Saprolegnia ferox causes the well-known salmon disease. *Empusa muscae*, the fungus that destroys house-flies, was at one time considered to be an aerial condition of *S. ferox*; it is now proved that the two are in no way related to each other.

Pythium debaryanum causes the damping off of seedlings of cress and other plants when sown in damp, dull situations. *Leptomitis lacteus* is not uncommon in rivers and streams, and often becomes a nuisance in places where organic matter or refuse is emptied into a stream from manufactories. It grows in long, dense tufts, resembling loose strands of tow in appearance and colour. Under the microscope it is at once recognised by the constrictions occurring at intervals in the hyphae, which are branched.

Distribution general.

Brefeld, *Bot. Unters. Schimmelpilze*, 'Studies on various Members of the Phycomycetes.' Vols. 1, 4, 6, 9.

Dangeard, 'Researches on Structure and Sexuality of *Polyphagus euglenae*,' *Le Botaniste*, 1 Aug. 1900.

Engler and Prantl, 'Phycomycetes,' *Pflanzenfam.*, 1, 1, p. 63 (1892).

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Saccardo, 'Phycomyceteae,' *Sacc. Syll.*, 6, 1, p. 181 (1888).

Thaxter, 'The Entomophthoraceae of the United States,' *Memb. Boston Soc. Nat. Hist.*, 4, p. 133 (1888).

Thaxter, 'Important Contributions relating to aquatic Fungi, more especially the Saprolegniaceae,' *Bot. Gaz.*, 21, p. 45 (1896); 21, p. 317 (1896); 20, p. 477 (1895); 20, p. 433 (1895); 19, p. 49 (1894).

Thaxter, 'Contributions to Morphology and Classification of the Zygomycetes,' *Bot. Gaz.*, 20, p. 513 (1895); 24, p. 1 (1897).

Wildeman, 'Census Chytridinearum; all known species, distribution, etc., includes 47 genera and 232 species,' *Bull. Soc. Roy. de Bot. de Belg.*, 35, p. 7 (1896).

HEMIASCOMYCETES

This group, under the name of Hemiasci, was established by Brefeld, who considers it as forming a transition between Phycomycetes and Ascomycetes, due to the conversion of the sporangium of the former into the ascus of the latter group. Those species having a variable number of spores in the ascus are here included, whereas when the spores in an ascus are constant in number, usually eight, the fungus belongs to the Ascomycetes proper.

As previously stated, Harper does not admit the conversion of sporangia into asci, but Harper's reasons for this denial were founded on too slender evidence, and his own definition of the origin of sporangiospores and ascospores respectively has broken down. At the same time no one has proved that the ascus is the outcome of a modified sporangium, although Dangeard has indicated that a new genus discovered by him, and named *Protascus*, but not yet definitely described, is said to support Brefeld's view.

Brefeld includes *Protomyces*, *Ascoidea*, and *Thelebolus*, in the Hemiascomycetes; other authors have also from time to time suggested the inclusion of other genera, but the whole subject is in an unsatisfactory condition, and the Hemiasci forms at present a sort of dumping-ground for forms approaching the Ascomycetes, but not coinciding with preconceived ideas bearing on classification.

Salmon and myself have given reasons for including the genus *Thelebolus* in the Ascomycetes, the principal of which are: the undoubted presence of from one to three asci enclosed within the pseudoparenchymatous outer protective covering; the origin of this protective covering or open perithecium from several cells, and not from a single cell, homologous with the sporangiophore as stated by Brefeld; the ascus is at first uninucleate in *Thelebolus*, and not multinucleate as in sporangia; finally, the variability in the size of the ascus, and in the contained number of spores, is not greater than in *Ryparobius* and allied genera, included by Brefeld in the Ascomycetes, and closely allied, if even generically distinct, from *Thelebolus*.

Protomyces does not appear to belong to the Hemiasci, even from Brefeld's point of view.

The genus *Ascoidea*, founded by Brefeld, is a remarkable form which certainly does not suggest a primitive stage. The entire mass consists of a more or less cushion-shaped body of a reddish colour up to 3 cm. long by 12 mm. thick. Long, straggling branched, rather closely septate hyphae, bear groups of oblong one-celled conidia at or near the ends of the branchlets, the tip of the branchlet being often terminated by a structure considered as an ascus by Brefeld. This ascus is elliptic-oblong, and contains myriads of minute spores which escape through an apical opening in the form of a long tendril consisting of the spores held together by mucus, much the same as in species of *Phoma*, etc.

Several such asci are formed from the tip of the same branchlet in succession, the empty asci persisting and forming a series of sheaths enclosing the central last-formed ascus. This condition of things prevails in connection with the development of the zoosporangia of certain species of *Saprolegnia*.

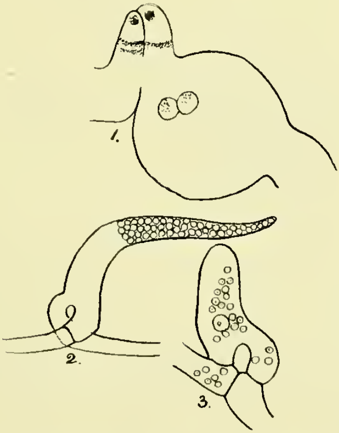

Fig. 63.—*Basidiobolus ranarum*, nuclei in beaks becoming disorganised : the male nucleus has passed into the enlarged female gamete, and has approached the female nucleus (after Fairchild). 2-3, *Dipodascus albidus*; 2, showing the mature ascus containing numerous spores (after Lagerheim); 3, young ascus of *D. albidus*, showing the one large nucleus which by division forms the nuclei of the spores (after Juel). All highly mag.

The fungus was discovered on a fallen trunk in a beechwood in Germany.

Such genera as *Basidiobolus*, *Dipodascus*, *Ascoidea*, etc., belong here, and in addition I have included those families in which the perithecium is either rudimentary or absent.

Brefeld, *Unters. Mykol.*, 9 (1891).
Dangeard, *Le Botaniste*, Dec. 1903, p. 23.
Massee and Salmon, *Ann. Bot.* 15, p. 315 (1901).

KEY TO THE FAMILIES

Perithecium rudimentary, consisting of a loose plexus of simple or branched hyphae, sometimes bearing specialised appendages. *Gymnoasceae.*

Perithecium entirely absent. Parasitic on the higher plants. Asci forming a continuous stratum on the surface of the infected portion of the host. *Exoasceae.*

Perithecium entirely absent. Plant consisting of a single cell. Asexual reproduction by budding. Conjugation of two cells previous to formation of ascospores occurs in some species. Mostly aquatic. *Saccharomyceteae.*

Gymnoasceae

A small group of somewhat primitive forms including about half-a-dozen genera. The species are all very minute, and grow on dung, dead vegetable substances, old bees' nests, and one species is parasitic on dogs' skin. The colour is usually clear and often bright orange, red, or yellow, and under a pocket-lens the plants resemble very minute tufts of down, sometimes furnished with rigid projecting spines, recalling to mind the appendages arising from the perithecia in members of the Perisporieae.

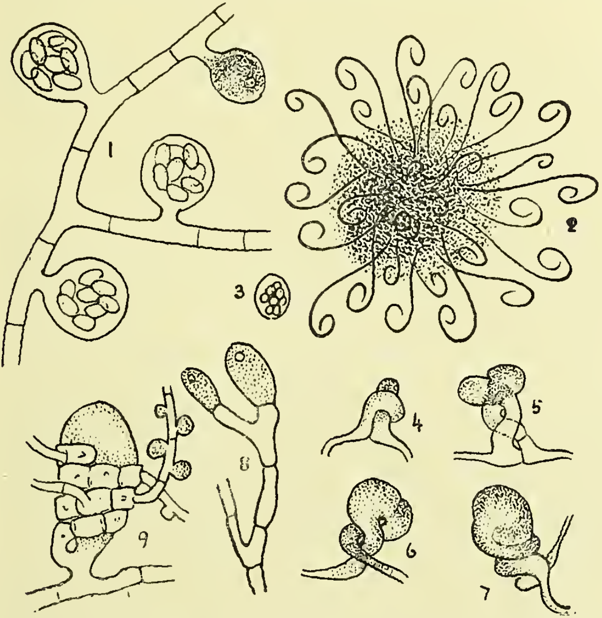

FIG. 64.—1, *Endomyces coprophilus*; 2, *Myxotrichum uncinatum*, an entire plant; 3, ascus with eight spores of *M. uncinatum*; 4, *Gymnoascus Reessii*, early stage in the formation of sexual organs; 5, more advanced stage of fig. 4, showing the sexual organs more twisted round one another; 6 and 7, more advanced stages of fig. 4, showing surface views of conjugating cells; in fig. 6 the two cells are of the same shape and size; in fig. 7 one is larger: both cells are coiled; 8, *Gymnoascus ruber*, young stage of reproductive bodies; 9, older stage of *G. ruber*, with one cell coiled round the other, and giving origin to ascogenous hyphae. Figs. 4-7 (after Dale). All highly mag.

The perithecium is very rudimentary, consisting in the most highly differentiated condition of a more or less loose weft of much-branched hyphae, certain of the branches becoming transformed into specialised appendages as stated above. This condition of things is met with in the genera *Gymnoascus* and *Ctenomyces*. In *Arachniotus* the perithecium is represented by a few simple or slightly branched hyphae, and special appendages are absent. A dense cluster of asci, or free spores, if the asci have disappeared, are located within the primitive perithecium.

According to Dale, a true sexual mode of reproduction is present. In *Gymnoascus Reessii* two branches spring up at right angles from a hypha, one on each side of a septum, and twist round one another once or twice. Their free ends become swollen, and each is cut off from its support by a cross-wall. These two cells become closely applied to each other, the walls separating them break down, and the two cells fuse. One of the two fused cells, termed the sterile cell [=male cell], is usually larger than the other—the ascogonium. The latter coils round the sterile cell, becomes septate, and most of the segments give origin to short, thick branches which themselves become branched. These are the ascogenous hyphae, and their tips become swollen and form the minute globose asci. At the time of conjugation both cells contain large numbers of nuclei, and after fusion the protoplasm and nuclei of the two cells become mingled. Doubtless a nuclear fusion now takes place, although this was not determined with certainty. Certain appearances suggest a nuclear fusion in the spores like that occurring in the Uredineae.

In *Gymnoascus setosus* the ascospores, on germination, produce one or two germ-tubes which soon branch and give origin to conidia by budding. When these conidia are sown in a hanging drop they begin to produce buds at once, as in the Saccharomyceteae. In *Arachniotus candidus*, in addition to a sexual mode of reproduction, oidia are produced by the breaking up into minute reproductive bodies of branched hyphae.

The Gymnoasceae are considered to show affinity with *Onygena*, as indicated by Ward's researches on the last-named genus.

Most abundant in Europe, but probably widely distributed.

Dale, *Ann. Bot.*, 17, p. 571 (1903).
Eidam, *Cohn's Beitr.*, 3, p. 385 (1883).
Ward, *Phil. Trans. Roy. Soc.*, ser. B., 191, p. 269 (1899).

Exoasceae

Parasitic on living plants. Mycelium mostly subcuticular, rarely penetrating deeper into the tissues, intracellular. A plexus of hyphae is developed just below the cuticle, which becomes differentiated into ascogenous and vegetative hyphae. The ascogenous hyphae develop directly into asci which rupture the cuticle and form a palisade-like arrangement of asci standing side by side on the surface of the matrix, entirely devoid of any perithecium or covering of any kind. In some instances the ascogenous cell grows out at once into the ascus, in other cases the ascus is separated from the cavity of the ascogenous cell by a transverse septum.

In *Exoascus* the mycelium is perennial in the tissue of the host. In *Taphrina* the mycelium is localised in deciduous organs, and is annual in duration. The spores are hyaline and one-celled, 4-6 in an ascus. In *Taphrina* the spores reproduce by budding after the manner of

FIG. 65.—*Exoascus deformans*, a very destructive parasite, causing the disease of peach leaves known as 'leaf-curl.' 1, two peach leaves distorted and coloured by the fungus; 2, section of portion of a diseased leaf, showing the asci of the fungus, *a*, ascus containing spores; 3, spores free from the ascus producing secondary spores by budding. There are at first eight spores in each ascus, but by a process of budding each spore produces numerous very minute secondary spores, so that eventually the ascus is filled with secondary spores. Fig. 1, nat. size; figs. 2 and 3, mag.

yeasts while yet in the ascus, which results in the ascus finally becoming crowded with a large number of minute secondary spores.

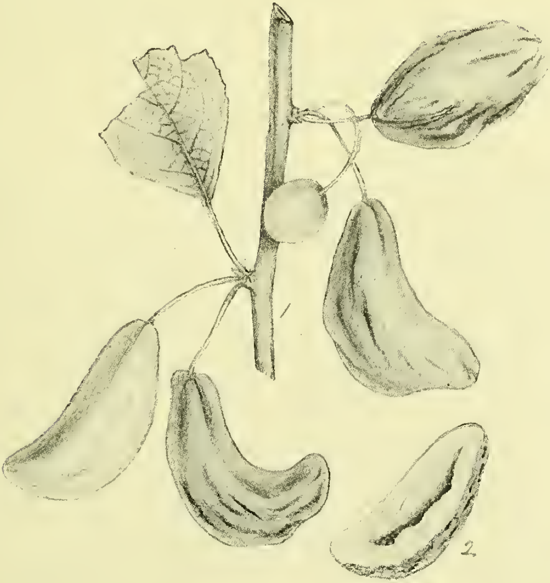

FIG. 66.—*Exoascus pruni*, a parasite attacking plums, causing distortion of the fruit. 1, portion of branch of a plum-tree bearing three diseased plums; 2, section through a diseased plum. Slightly reduced.

Many species are injurious parasites, as 'Peach leaf-curl, 'Plum-pockets,' etc. Some species cause the formation known as 'witches' brooms.' Most abundant in Europe, but probably widely distributed.

Engler and Prantl, *Pflanzenfam*, *Exoascaceae*, 1, 1, p. 158 (1894).

Sadebeck, *Unters. über d. Pilzgattung Exoascus*, *Jahresb. der wissensch. Anst. zu Hamburg*, No. 1 (1883).

Sadebeck, *Die Parasitischen Exoasceen*, *Jahrb. d. Hamburg wissensch. Anst.*, 10 (1893).

Saccharomyceteae

Probably no group of fungi has received more attention than the present, mostly on account of the fermentative power of many species, which render them of great importance from an economic standpoint. The liberation of carbonic acid gas is utilised in the bakery, and the formation of alcohol, a by-product of metabolism, is of equal importance in the brewery. Some wild yeasts cause fermentation on the surface of ripe fruits.

The yeast-plant is a very simple organism, consisting typically of a single cell. *Saccharomyces Ludwigii* and some other species sometimes produce a rudimentary form of mycelium. Two modes of reproduction are known: a purely vegetative method known as budding, and a more complicated method by the formation of endospores. A third method is said to occur in some species, where the cell-wall becomes thickened and hardened, practically forming chlamydospores.

When placed in a nutrient solution at a suitable temperature, budding takes place with great rapidity, the solution soon becoming turbid owing to the increase in quantity of yeast-cells. Slight papillae appear at various points on the surface of a cell, these papillae increase in size, and are soon attached to the parent-cell by a narrow neck, and finally fall away, when they soon repeat the process of budding. When growth is very active, the daughter-cells often give off buds before they separate from the parent-cell, and it is not unusual to find buds of various sizes and ages representing different generations, adhering in a chain.

Endospores are formed only under certain conditions. The most important of these, according to Hansen, are, that the yeast-cells must be placed on a moist, porous surface, and have a plentiful supply of air. The most suitable temperature is about 25° C.; only young and vigorous cells should be used for the experiment. Blocks of gypsum, slices of carrot, and pads of blotting-paper soaked in a solution of sugar have respectively proved

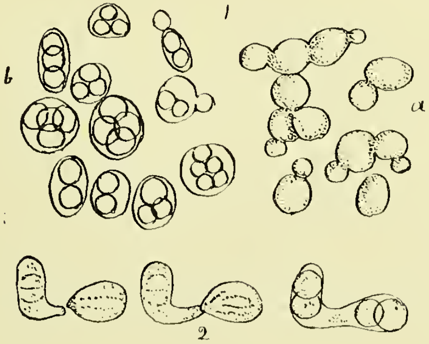

FIG. 67.—1, *Saccharomyces cerevisiae*; *a*, reproduction by budding or gemmation; *b*, cells containing ascospores. 2, *Zygosaccharomyces Barkeri*, showing stages in the conjugation of two cells; in the right-hand fig. four ascospores are present. (Fig. 1 after Hansen, fig. 2 after Barker.) All highly mag.

suitable for this work. Wager placed compressed yeast in a tumbler containing a five per cent. saccharose solution in water; a scum soon formed on the surface, and as evaporation proceeded, the cells that were left on the side of the glass produced endospores. The number of endospores varies from two to four, the latter number being most frequent. So far as is at present known, endospores in species of *Saccharomyces* are produced by free-cell formation without the intervention of any sexual process. In some other genera, however, a true sexual act precedes the formation of endospores. Barker has shown that in a genus he has called *Zygosaccharomyces*, conjugation of two cells precedes the formation of endospores. Two cells lying close together produce small, bud-like outgrowths opposite to each other; these continue to grow into beak-like structures until they meet. The walls dissolve at the point of contact, and communication between the two cells is effected. After fusion of the two cells is completed, the protoplasm in each cell undergoes certain changes and becomes contracted into two spheres, which finally develop into spores surrounded by a distinct cell-wall. The number of spores produced is variable, two in each mother-cell being the most usual number. A fusion of two nuclei after conjugation, and the subsequent division of the fusion-nucleus to form the nuclei of the spores, was observed. Ordinary vegetative budding also occurs, exactly as in *S. cerevisiae.*

In the genus *Schizosaccharomyces*, described by Beyerinck, in which, in place of budding, when a cell reaches a given size, a transverse septum is formed, and the two daughter-cells become separated by the splitting of the septum, hence the generic name. Guilliermond has shown that in *Schizosaccharomycetes* a simple form of sexual reproduction is also present. Two adjoining cells put out protuberances that meet and fuse, the cell-wall disappearing at the point of junction. Eventually the neck expands and with the two conjugating cells forms a large oval cell, or in some instances the neck does not expand, and a more or less hour-glass form results. A nucleus from each conjugating cell passes in to the neck, and these two fuse when fusion of the cells has taken place. The fusion-nucleus afterwards divides to form two daughter-nuclei, which by repeated division form the nuclei of the spores.

In *Schizosaccharomycetes octosporus* eight spores are constantly present in the ascus.

The cell containing endogenously formed spores is considered as an ascus, hence the Saccharomycetes are included, in the wider sense, in the Ascomycetes, but on account of the entire absence of a perithecium or protective covering are grouped with the Hemiascomycetes, their nearest affinity being with some of the simpler genera—as Endomyces, included in the Gymnoasceae.

The question as to the presence of nuclei in yeast has been much discussed of late. Wager has investigated this matter in an exhaustive manner. The following is his summary :—

'1. All cells of yeast contain a nuclear apparatus.

'2. In the earlier stages of fermentation this consists of a nucleolus in close contact with a vacuole which contains a granular chromatin-network, and exhibits a structure in many cases like the chromatin-network of the nuclei of the higher plants.

'3. In the latter stages of fermentation the chromatin-containing vacuole may disappear, its place being taken by a granular network or a number of chromatin granules, which may be disseminated through the protoplasm, or grouped around the nucleolus.

'4. The nucleolus is present in all cells. It appears to be a perfectly homogeneous body, which may, however, at times appear granular owing to the granules around it.

'5. In young cells numerous chromatin-vacuoles are often found. These appear to fuse together to form the single vacuole which occurs in cells during the early, and sometimes later, stages of fermentation.

'6. In the process of budding, the division of the nuclear apparatus does not exhibit any definite stages of karyokinesis. It must, I think, be regarded as a direct division of the nucleolus into two equal or nearly equal parts, accompanied by division of the chromatin-vacuole, network, or granules.

'7. The nucleolus divides either in the neck joining the bud to the mother-cell, or more rarely in the mother-cell itself, one of the products of division passing subsequently into the bud.

'8. In spore formation the chromatin disseminated through the protoplasm becomes absorbed more or less completely into the nucleolus, which then divides by elongation and constriction into two. During the division deeply stained granules (chromosomes?) appear surrounded by a less deeply stained substance, which remains for a time connecting the two daughter-nucleoli together. This may perhaps indicate a simple, intermediate stage of karyokinesis.

'9. Subsequent divisions take place, resulting in the formation of four (sometimes more) nucleoli. Each nucleolus becomes surrounded by protoplasm and a delicate membrane, and thus the spores are formed standing free in the remainder of the protoplasm.

‘10. The spores are at first very small, but they soon increase in size; the surrounding protoplasm becomes used up; the spore membranes increase in thickness until at last in the mature condition they completely fill the mother-cell.

‘11. In *S. Ludwigii* and *S. pastorianus* the structure of the nuclear apparatus is similar to that in *S. cerevisiae*, and its division during the process of budding appears to be also the same.’

The above remarks apply more especially to *S. cerevisiae*, *S. cerevisiae* — Hansen 1, *S. Ludwigii*, *S. pastorianus*, *S. Mycoderma*. Compressed yeast, and a red yeast found in the air of the laboratory, were also examined.

Büchner has shown that the alcoholic fermentation of sugar induced by yeast is due to the activity of an enzyme or soluble ferment, which, by a special method of treatment, can be extracted from the yeast-cell. Green has corroborated this observation, and points out that the enzyme is only secreted while the yeast-cells are active, or during actual fermentation.

Symbiotic relationship between yeasts and bacteria is not uncommon, and such dual compounds not unfrequently promote fermentation. Kephir, a derivative of milk, and a weakly alcoholic effervescing beverage, usually made from mare’s milk, has been used for centuries in the Caucasus. The ‘kephir grains’ with which it is prepared contain both a bacterium and a yeast. The yeast cells secrete an enzyme (lactase) that converts the milk sugar into grape sugar, which is then further broken up by fermentation into alcohol and carbonic acid. The lactic acid bacteria precipitate the casein as a flocculent substance, easy of digestion, and also impart a pleasant acid flavour to the liquor.

Tibi, a substance found on the stems of species of Cactus in Mexico, and used for producing a fermented beverage, has been shown by Lutz to consist of a bacterium and a yeast in symbiotic union. Ward has also shown that the production of ginger-beer is due to the work of bacteria and yeast-cells respectively, and suggests a symbiotic condition between the two organisms.

Barker, *Phil. Trans. Roy. Soc.*, 194, p. 467 (1901).

„ *Journ. Federated Inst. of Brewing*, 8, p. 26 (1902).

Beyerinck, *Centralbl. für Bakter-u. Parasitenkunde*, 16, p. 49.

Büchner, *Ber. d. deutsch. chem. Gesell.*, 30, p. 117 (1897).

Green, *Ann. Bot.*, 12, p. 491 (1898).

Hansen, *Meddels. fra Carls. Lab.*, 2, p. 152.

„ *C. R. Trav. Lab. Carlsberg*, 5, p. 1 (1900).

Jörgensen, *Micro-organisms of Fermentation*, London (1899).

Lutz, *Bull. Soc. Myc. France*, 15, p. 157 (1899).

Ward, *Trans. Phil. Roy. Soc.*, 183, p. 125 (1893).

Wager, *Ann. Bot.*, 12, p. 449 (1898).

ASCOMYCETES

The enormous assemblage of species included in the present Order agree in having a definite number of spores —usually eight—produced by free-cell formation in a

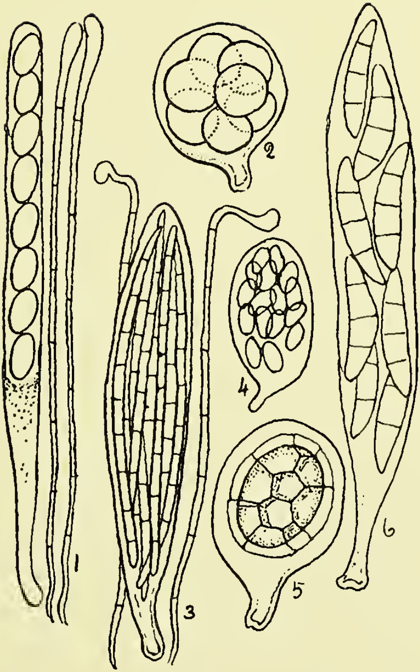

FIG. 68.—Typical forms of asci. 1, ascus containing eight spores in uniseriate order, and accompanied by two paraphyses, of *Peziza cerea*; 2, *Sphaerosoma Leveillei*; 3, *Geoglossum Peckianum*, eight long multiseptate spores arranged in a fascicle: the paraphyses are curved at the tip; 4, *Ryparobius sexdecemsporus*, ascus containing sixteen spores; 5, *Tuber excavatum*, ascus containing one large spore: some asci contain two somewhat smaller spores; 6, *Zignoella corticola*, containing eight triseptate spores, irregularly biseriate in arrangement.

mother-cell called an ascus. In the greatest number of species the ascus is elongated and narrowly cylindrical, and the spores are arranged in a single row in the upper half of the ascus. In others, again, the asci are broader in proportion to their length, and the spores more or less arranged in two rows. Departures from the most frequent type are not uncommon. In the Tuberaceae the asci are frequently globose, and contain a variable number of spores, and frequently fewer than eight.

In certain other species the ascus may contain sixteen, thirty-two, forty-eight, or an indefinite number of spores. In known cases the asci originate from hyphae that spring, usually in considerable numbers, from a specialised cell or oogonium, which certainly in some instances is a sexual cell that requires to be fertilised before it gives origin to the ascogenous hyphae. On the other hand, the paraphyses and hyphae forming the perithecium or protective portion of the fruit never originate from the sexual cell producing ascigerous hyphae, but from other cells of the hypha bearing the sexual cell, and situated immediately below it.

The spores may be colourless or coloured at maturity, globose, elliptical, fusiform, or needle-shaped; the surface may be smooth, spinulose, warted, or covered with a raised network.

In the Saccharomycetes a single cell constitutes an individual, hence in this family a protective structure or perithecium, so characteristic of the group, is absent. In the Gymnoasceae the peridium consists of very loosely interwoven hyphae, which are often curiously branched, and in some species bear specialised appendages, recalling to mind the somewhat similar appendages springing from the perithecia of many forms of the Perisporieae.

Conidial forms are numerous throughout the group, and are very diversified in form and structure, and consequently have received special names without end. In many instances conidial stages have been proved to be an integral part of an ascigerous form, by the only certain proof, that of producing the conidial from the ascigerous form and *vice versâ*. In the majority of instances, however, relationship between two forms is only assumed, the evidence being that of contiguity, or the constant sequence of two or more forms.

The whole of the large assemblage of forms included under 'Fungi imperfecti,' including the Hyphomycetes, Melanconieae, and Sphaeropsideae, are usually considered as hitherto unattached conidial forms of the Pyrenomycetes.

The Order includes two sub-orders, Pyrenomycetes and Discomycetes.

KEY TO THE SUB-ORDERS

Hymenium or ascus-bearing surface permanently enclosed in a hollow sporophore or perithecium, usually furnished with a small ostiolum or opening, through which the spores escape at maturity. When no specialised opening exists, the sporophore eventually ruptures irregularly, thus allowing the spores to escape. *Pyrenomycetes.*

Hymenium or ascus-bearing surface fully exposed at maturity, borne on a flat or cup-shaped sporophore. *Discomycetes.*

In typical examples the two groups are readily recognised, the most general form of perithecium in the Pyrenomycetes resembling a flask with a very short neck, the ostiolum or opening for the escape of the spores being situated at the apex of the neck. Sometimes these perithecia are isolated, each one being an entity, as in *Sphaeria*. In other examples, as *Xylaria*, numerous perithecia are embedded in the periphery of a more or less fleshy stroma, their stomata for the escape of the spores opening on the free surface of the stroma. This structure may be considered as a compound *Sphaeria*, in the sense of numerous perithecia (independent plants) in *Sphaeria*, being grouped together on a stroma, the whole forming a plant, in *Xylaria*. In some genera, as *Nectria*, the entire sequence from where one perithecium constitutes a plant, to others where numerous perithecia embedded in a stroma represents an individual, is met with. In other genera, as *Gnomonia*, not uncommon on dead hazel leaves, the neck of the perithecium is very much elongated and hair-like; whereas in *Nectria* the neck is entirely suppressed, and the minute ostiolum is situated at the apex of the more or less globose perithecium. In some cases the surface of a free perithecium is minutely downy, at others covered with stout, spine-like structures, whereas in the Perisporieae the perithecia often bear much-branched, highly specialised hyphae called appendages, the function of which is not known.

In the Discomycetes the ascophore is typically shallowly cup-shaped, with or without a distinct stem. The ascophore or cup, as it is often called, usually has the margin strongly incurved when young, but this gradually expands, exposing the circular hymenium or disc. The only good example of a stroma in the Discomycetes is met with in the genus *Cyttaria*, where the general appearance of the fungus is that of a morel (*Morchella*), but in *Cyttaria* the pear-shaped mass, three to six centimetres long, must be considered as a fleshy stroma, bearing numerous ascophores embedded in its periphery. In some instances, as the Sticteae, where the species are embedded in the matrix, the ascophore is quite rudimentary. Other species embedded in the substratum depart from the typical circular disc or hymenium, and have an elongated or radiately formed sporophore, which splits along its length; the lips of the split finally gape and expose the hymenium.

As would be expected in such a large assemblage of forms, the two groups closely approach each other at certain points. Genera and even families have from time to time been removed from one sub-order to another, depending on individual opinion.

The family Hysterieae has until quite recently been considered as belonging to the Discomycetes. Saccardo, however, has removed it to the Pyrenomycetes. The sporophore is more or less elongated, or sometimes radially branched, and the opening of what must be considered a perithecium from Saccardo's point of view has an elongated slit through which the spores escape. Now, technically, the ascus-bearing surface or disc should remain perfectly concealed in the Pyrenomycetes, whereas in many of the Hysterieae the disc is partially exposed by the gaping of the border or lips bounding the slit. Hysterieae is a transition family, undoubtedly, and it was not worth the trouble on Saccardo's part to remove it from one subfamily to another.

The genus *Sphaerosoma* is also a transition genus connecting the Tuberaceae with the Discomycetes. It has the hymenial structure and asci of the Discomycetes, but more or less of the general morphology and certain of the important characteristics of the Tuberaceae. It is more or less subterranean in habit, and has a continuous, more or less globose peridium which permanently conceals the hymenium from view. It has occupied a place in the Tuberaceae until quite recently, when it was placed at the commencement of the Discomycetes by Saccardo.

PYRENOMYCETES

KEY TO THE FAMILIES

Ostiolum or mouth, when present, circular.

Perithecia produced singly, that is, not aggregated in a stroma, substance thin, membranaceous, or in some instances subcarbonaceous; completely closed, hence the structure must decay or become irregularly torn before the spores can escape. *Perisporieae.*

Perithecia produced singly or aggregated in a stroma, substance membranaceous, coriaceous, or distinctly carbonaceous, blackish, quite distinct in structure from the stroma, when the latter is present; dehiscing by a definitely formed opening or ostiolum. *Sphaerieae.*

Perithecia scattered or aggregated in a stroma, fleshy or membranaceous, not carbonaceous and frigid, generally reddish, rarely bluish or yellowish-olive, with a distinct ostiolum. Stroma, when present, rather soft and fleshy, rarely byssoid. *Hypocreae.*

Perithecia immersed in a stroma from which they are scarcely or not at all differentiated; stroma cushion-shaped, effused or linear, coriaceous or carbonaceous (not fleshy), blackish (not brightly coloured); asci 4-8 spored, spores hyaline, rarely tinged brown. *Dothidieae.*

Perithecia scattered, not in a stroma, subsuperficial, blackish, membranaceous or carbonaceous, much flattened, formed of radiating hyphae; ostiolum present or absent. *Microthyrieae.*

Ostiolum or mouth, when present, distinctly elongated.

Perithecia scattered, not in a stroma, subsuperficial or at first covered by the epidermis, carbonaceous, ostiolum formed of two elongated lip-like ridges, with a very narrow crack through which the spores escape. *Lophiostomeae.*

Perithecia scattered, not in a stroma, erumpent, becoming superficial, coriaceous or carbonaceous, generally blackish, elongated, sometimes standing up on edge, ostiolum elongated, the entire length of the perithecium, bounded by lip-like ridges on either side, *Hystericae.*

Ascophore irregularly globose, subterranean or rarely almost on the surface of the ground, indehiscent, fleshy. *Tuberaceae.*

Stroma minute, wart-like; cavities or loculi minute, numerous, containing one ascus each; asci subglobose, 8-spored. *Phymatosphaerieae.*

Perisporieae

Perithecia membranaceous, or in some forms rigid and carbonaceous, produced singly, completely closed, spores liberated on the decay or rupture of the wall. Conidial forms not unusual. Mostly growing on living plants, many of the species being amongst the most destructive of fungus parasites. On account of the closed perithecia the present family is considered by some authors as having affinity with the Tuberaceae.

Distribution cosmopolitan.

KEY TO SUB-FAMILIES

Parasitic. Mycelium generally superficial, whitish, sending haustoria into the epidermal cells of the host-plant. Perithecia membranaceous, bearing various forms of highly specialised hyphae or appendages. Conidia usually produced in chains, springing from the superficial mycelium (= *Oidium*). *Erysipheae.*

Parasitic or saprophytic. Mycelium black. Perithecia subglobose or depressed, sometimes bearing appendages. Conidia sometimes present, but not of the Oidium type. *Perisporieae.*

Perithecia more or less conical, simple or branched, eventually becoming torn at the apex and forming an opening through which the spores escape; seated on a thick, black mycelium that readily peels off the matrix. Conidia are present. *Capnodieae.*

Erysipheae

All known species are obligate parasites on chlorophyllose plants. The vegetative mycelium is superficial and nourished by means of numerous haustoria which penetrate the epidermal cells of the host-plant.

Exceptions to the above general statement are met with in the genera *Phyllactinia* and *Erysiphe.* In the first mentioned Palla has shown that in *P. suffulta* certain hyphae originating from the superficial mycelium enter through stomata of the host, extend for a short distance in the intercellular spaces, and send haustoria into the adjoining

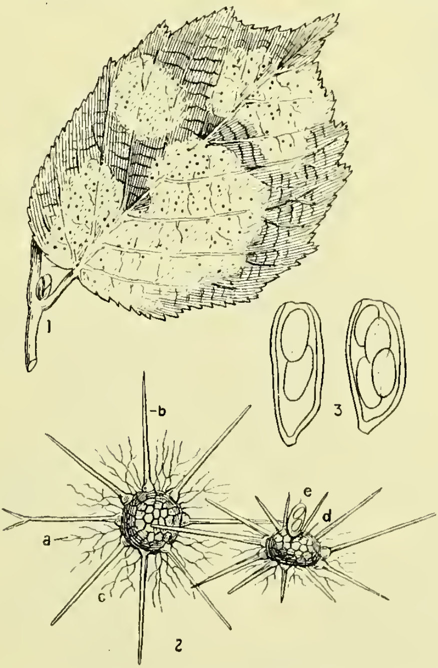

FIG. 69. —*Phyllactinia suffulta*, a fungus having superficial mycelium which grows on the surface of the host-plant. 1, a hazel leaf partly covered with the white mycelium of the fungus; 2, fruit of the fungus furnished with spine-like, projecting appendages; 3, asci containing spores. All, except fig. 1, mag.

cells. Salmon has shown that in *Erysiphe taurica*, the whole of the mycelium during the conidial stage is located in the tissues of the host, the conidiophores emerging

FIG. 70.—*Uncinula spiralis*, a destructive parasite to the vine. 1, conidial stage forming white patches on the upper surface of a vine leaf; 2, part of a vine leaf with the ascigerous form of the fungus; 3, portion of mycelium bearing erect chains of conidia at *a*, *a*; and haustoria which penetrate into the living cells of the leaf, *b*, *b*; 4, a single free conidium; 5, a perithecium with its curled appendages; 6, an ascus containing six spores; 7, a free ascospore; 8, grapes attacked by the fungus. Figs. 1, 2, and 8, somewhat reduced; the remainder mag.

through the stomata into the air, after the manner of *Ramularia* and other leaf parasites.

The mycelium is white and forms a delicate white felt on living leaves, young shoots, and fruit, and is popularly known as mildew. The conidia are one-celled, more or less cylindrical, and most frequently produced in chains at the tips of slender, erect conidiophores, which are simple

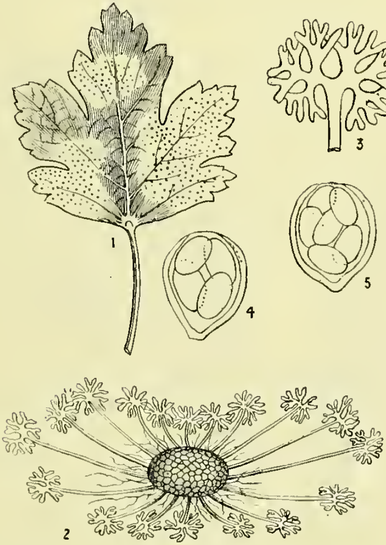

FIG. 71. — *Microsphaeria grossulariae,* a parasite on the gooseberry plant. 1, gooseberry leaf with white patches of the conidial form of the fungus: the minute black points are perithecia; 2, a perithecium with its appendages; 3, the branched tip of an appendage; 4, 5, asci containing spores. Fig. 1, nat. size; the remainder highly mag.

in all known species except *Erysiphe taurica*, where they are slightly branched.

The conidial form of reproduction was at one time considered as an entity, and called *Oidium*.

FIG. 72.—*Meliola*, the superficial black mycelium forming black patches on orange leaves. Nat. size.

Later in the season the sexual ascigerous form of fruit is formed on the superficial mycelium, in which it nestles under the form of minute, yellowish balls, which become black when mature. The perithecia bear specialised hyphae which are often much branched or curled at the tip.

The spores are colourless and one-celled, and in some genera vary in number in different asci from the same perithecium, a feature also common in the Tuberaceae.

Distribution cosmopolitan.

Perisporieae

The perithecia are usually black, but in some genera, as *Eurotium*, they are yellow or reddish. Many species are parasites, occurring most frequently on leaves or fruit, where they form black patches, or sometimes almost cover the surface with a black film. Conidial forms are known. The mould called *Aspergillus* is the conidial condition of *Eurotium*.

Most abundant in warm regions.

Capnodieae

All grow on living leaves, stems, or fruit; they are most abundant on coriaceous, persistent leaves, and last for more than one season, when they form a thick, black crust, and prove injurious, owing to preventing the action of light on the surface of the leaves. As a rule, the species are not parasites, but commence growth more especially on leaves that are first covered with 'honey dew.' Both genera and species are imperfectly known. Several conidial phases are known, whereas the ascigerous condition is somewhat rare.

Most abundant in warm regions.

Sphaerieae

In the simple forms the perithecia are free, either quite superficial, partly immersed, or completely buried in the matrix, the beak or ostiolum alone reaching to the surface.

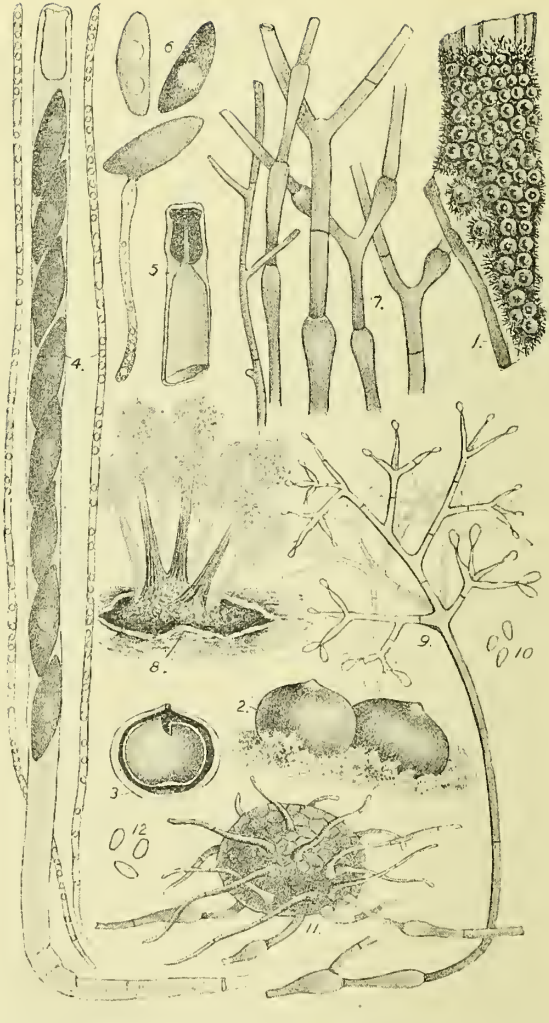

FIG. 73.—*Rosellinia radiciperda*, a typical Ascomycete showing conidial and ascigerous forms of fruit. 1, ascigerous stage of the fungus showing the sexual fruit or perithecia; 2, perithecia or sexual fruit on a

Description continued on p. 291.

In *Valsa* and allies many perithecia, closely packed together, are immersed in the matrix, the beak or ostiolum is elongated, and all the beaks converge and come through the matrix at one point. The common candle-snuff fungus, *Xylaria hypoxylon*, illustrates the type of vertical stroma so common in this family. The perithecia are immersed in the periphery of the stroma, having their mouths pointing outwards and opening on the free surface of the stroma. The upper portion of the stroma bears minute, colourless conidia. *Daldinia*, not uncommon on dead wood, has a globose stroma about the size of a walnut; the perithecia as usual are peripheral. The stroma is solid, dark brown, and marked with concentric zones. In *Eutype* there is a thin, crust-like, black stroma, which sometimes extends for several inches on dead wood or bark. The surface of the stroma is minutely asperate or rough, due to the slightly projecting mouths of the numerous perithecia. The spores are colourless or coloured, one-celled, or divided into two or more cells by the formation of septa.

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larger scale, showing the papilla at the apex, which is perforated for the escape of the spores; 3, section of perithecium, showing the wall to consist of two layers; 4, an ascus containing eight spores, also two paraphyses; 5, tip of an ascus after treatment with iodine, showing the arrangement for effecting the opening of the ascus, due to expansion of the dark portion, so as to admit of the escape of the spores; 6, ascospores, one of which is germinating; 7, brown mycelium with swellings at intervals: this peculiar swelling just below the septum is very characteristic of two or three allied parasitic species of Rosellinia; 8, a black sclerotium belonging to the fungus, bursting through the cortex of a root, and bearing several clusters of conidiophores bearing conidia; 9, a single conidiophore on a larger scale, showing the mode of branching: conidia are borne at the tips of the branchlets; 10, free conidia; 11, a pycnidium or second form of conidial fruit, in which the conidia or stylospores are produced in a conceptacle; 12, stylospores. Fig. 1, nat. size; the remainder highly mag.

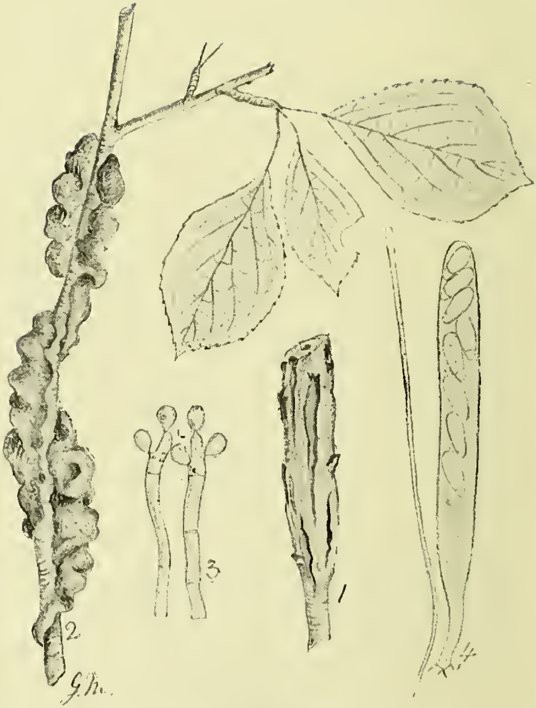

FIG. 74.—*Plowrightia morbosa*, a fungus with a large, irregularly shaped black stroma in the substance of which numerous perithecia containing spores are immersed. 1, portion of a branch of a plum-tree bearing a stroma of the fungus covered with conidia; 2, portion of a branch with a stroma of older date and bearing perithecia; 3, conidiophores with conidia near the tip; 4, ascus containing eight ascospores: by its side is a paraphysis. Figs. 1 and 2, half nat. size; the others mag.

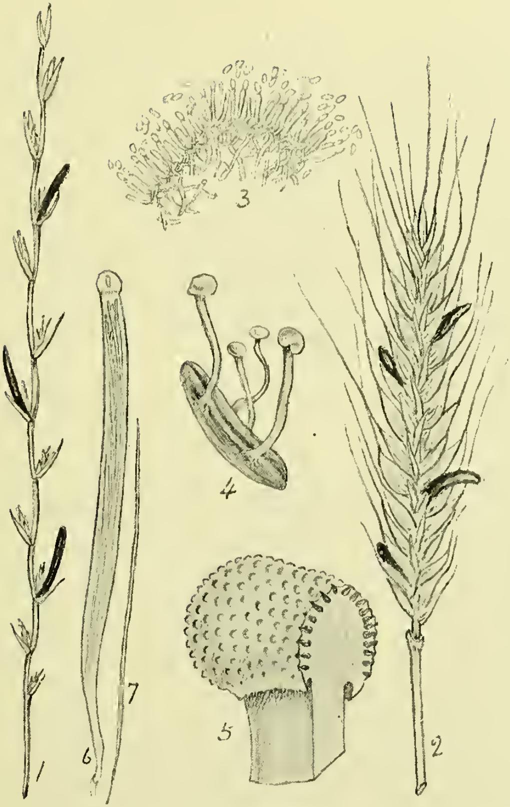

FIG. 75.—*Claviceps purpurea*, or ergot. 1, ergot on rye-grass; 2, ergot on rye: the black, horn-like bodies are stromata or sclerotia of the fungus, and bear the conidial form of fruit; 3, portion of conidial form of fruit produced on a stroma: the conidia are mixed with a sweet substance attractive to flies; 4, a stroma bearing the stalked ascigerous form of fruit, after lying on the ground throughout the winter; 5, head or fertile portion of ascigerous fruit, showing the warted surface due to the projecting mouths of the perithecia: the section shows the numerous perithecia sunk in the fleshy stroma; 6, an ascus containing eight needle-shaped spores; 7, a single spore. Figs. 1 and 2, nat size; the remainder mag.

The colour of the spores, and the number and arrangement of the septa, are the principal features used by Saccardo for the discrimination of genera throughout his work on the fungi.

The Sphaeriaceae are distinguished from the Perisporieae by the presence of an ostiolum; from the Hypocreae by the black or dusky perithecia, and their coriaceous or carbonaceous texture.

Most of the species are saprophytic on dead wood, bark, or leaves. Some, however, are destructive parasites.

Distribution general.

Hypocreae

The present family is characterised by the perithecia being of a comparatively soft and fleshy nature, never rigid and carbonaceous as in Sphaeriaceae. Furthermore, the perithecia are clearly coloured as a rule, red or orange being the predominating tint. This is well seen in species of *Nectria*. The spores escape through a definite ostiolum or mouth. The stroma, when present, is fairly soft and fleshy, sometimes brightly coloured as in some species of *Cordyceps*, where it is erect, more or less club-shaped, or resembling the inflorescence of the reed-mace in miniature. In some species of *Hypocrea* the stroma forms a fleshy, expanded, cushion-shaped mass. Asci commonly 8-spored, in a few instances 4-spored or many-spored. Spores generally hyaline, rarely brown. Conidial phases not uncommon.

Some species of *Nectria*, *Hypocrea*, *Claviceps*, *Hypocrella*, etc., are parasitic on higher plants; *Hypomyces* and species of *Claviceps* are parasites on other fungi; *Cordyceps* are parasitic on insects.

Widely distributed.

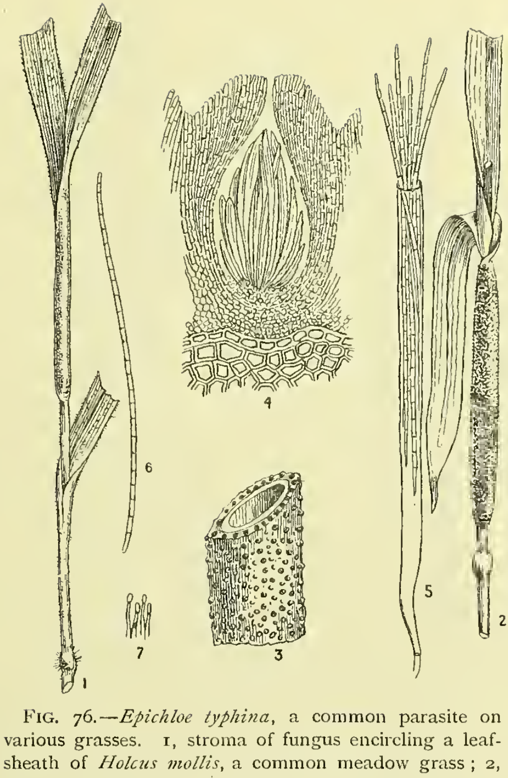

FIG. 76.—*Epichloe typhina*, a common parasite on various grasses. 1, stroma of fungus encircling a leaf-sheath of *Holcus mollis*, a common meadow grass; 2, stroma of the fungus encircling the leaf-sheath of *Holcus lanata*; 3, a portion of the stroma of the fungus showing the warted surface: the warts correspond to the mouths of the perithecia, which are sunk in the stroma; 4, section of a perithecium sunk in the substance of the fleshy stroma; 5, an ascus showing the spores escaping from its apex; 6, a single filiform or needle-shaped, many-septate spore; 7, conidiophores bearing conidia. Figs. 1 and 2, slightly reduced; remainder mag.

FIG. 77.—*Nectria ditissima*, a destructive parasite to apple-trees. 1, a branch recently attacked, the disease entered at the axil of the small branch, *a*, *a*, perithecia; 2, a branch that has been diseased for some time, showing a rugged callus formed round the wounds: the end of the broken branch, *a*, is the point where the fungus entered; 3, a section through a stroma containing perithecia, *a*, *a*, on its surface; 4, a single perithecium; 5, section of a perithecium; 6, portion of a stroma bearing conidia; 7, a conidium germinating; 8, portion of the contents of a perithecium; *a*, an ascus containing eight spores; *b*, *b*, paraphyses. Figs. 1 and 2, reduced; the remainder mag.

Dothidieae

In this family the perithecia are always immersed in a stroma. In the preceding families the perithecium has always a distinctly differentiated wall of its own, quite distinct from the substance of the stroma in which it appears as an independent structure inserted. In Dothidieae the perithecium has no such differentiated, circumscribing wall, hence the perithecia are sometimes called loculi or cells. The fleshy and brightly coloured or clear-coloured stroma separates Hypocreae from the present family.

Many species are parasitic on living leaves, where they form flattened or slightly convex patches of a shining black, giving the leaf the appearance of having been sprinkled with drops of pitch.

Distribution general.

Microthyrieae

Distinguished by the minute, black, free, scattered perithecia being remarkably flattened, and by the regularly radiating arrangement of the pseudoparenchymatous tissue of the perithecial wall. An ostiolum is present in some species, and obsolete or apparently absent in others.

Often growing as parasites on leaves, appearing under the form of minute black dots.

Widely distributed.

Lophiostomeae

The principal feature of the present family resides in the structure of the ostiolum, which is distinctly elongated; it is usually bounded by two parallel, thickish ridges, or lip-like bodies, between which the true ostiolum or opening, through which the spores escape from the perithecium at maturity, appears as a very narrow slit.

Appearing as minute black specks on wood, branches, and herbaceous stems. Mostly saprophytes.

Distribution general.

Hysterieae

Perithecia elongate, simple or branched, sometimes with several radiating arms, sometimes vertical, like a mussel-shell standing on its edge. Allied to Lophiostomaceae, differing mainly in the longer ostiolum, which runs the entire length of the perithecium as a slit or groove, usually bounded by thickened ridges or lips. This group was until recently included in the Discomycetes, but the coriaceous or carbonaceous perithecia, and often coloured and multiseptate spores, are considered by Saccardo to indicate a closer affinity to the Pyrenomycetes.

The majority are saprophytes, growing on wood or bark. A few are parasitic on living leaves and stems.

So far as at present known, most abundant in the northern hemisphere.

Tuberaceae

Ascophore subterranean, or in some species only imperfectly buried or growing amongst decaying leaves. More or less globose or irregularly nodulose, firm; the wall of the ascophore is sometimes continuous, in other species possessing an opening or perforation. The gleba is either compact or lacunose. In some genera the asci are cylindrical, in others nearly globose. The spores are often very large, having the exospore covered with warts, spines, or raised ridges anastomosing to form a network. In the genus *Elaphomyces* the spores form a black, powdery mass at maturity. Many species, as the common truffle, are

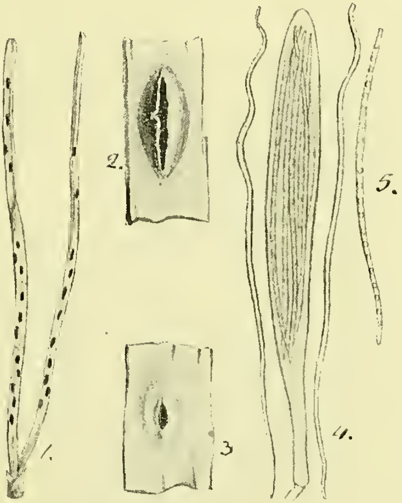

FIG. 78.—*Lophodermium pinastri*, a fungus parasitic on pine leaves. 1, pine leaves with the fungus forming minute, elongated black spots; 2, ascigerous form of the fungus; 3, spermogonium of the fungus; 4, ascus containing eight spores, two paraphyses are also present; 5, a single needle-shaped, multiseptate spore. Fig. 1, nat. size; remainder mag.

strongly scented. This provision enables rodents to detect their presence, when they are unearthed and greedily eaten; by this arrangement the spores are dispersed.

Some species are edible, and considered as luxuries. None are known to be poisonous.

Most of the known species are European, but their subterranean habit may account for our lack of knowledge respecting their distribution. Recently an enthusiastic collector has discovered a considerable number of species in Tasmania.

Phymatosphaerieae

A small family considered to be allied to the Tuberaceae from which they differ in aerial habit. The few known genera are mostly extra European.

DISCOMYCETES

Analysis of the Families.

A.—Ascophore superficial, fleshy, or waxy.

Parasitic. Ascophore globose or piriform, almost stemless, fleshy, and tough, periphery honeycomb-like. On trees. *Cyttarieae.*

Ascophore vertical, with a distinct stem, conical, clavate, or subglobose, fleshy or waxy, surface even, with brain-like folds or honeycomb-like. On the ground. *Helvelleae.*

Ascophore cup-shaped or discoid, fleshy or waxy, sessile or stalked, disc or hymenium even. Tips of asci not projecting beyond level of hymenium. Parasitic or saprophytic. *Pezizeae.*

Ascophore cup-shaped or discoid, fleshy, sessile. Asci projecting above level of hymenium. On dung. *Ascoboleae.*

B.—Erumpent and becoming almost superficial, tough, or gelatinous.

Ascophore cup-shaped or becoming almost plane, almost sessile or stipitate, often tufted from a common or stromatic base, tough or horny, usually scurfy outside.

Dermateae.

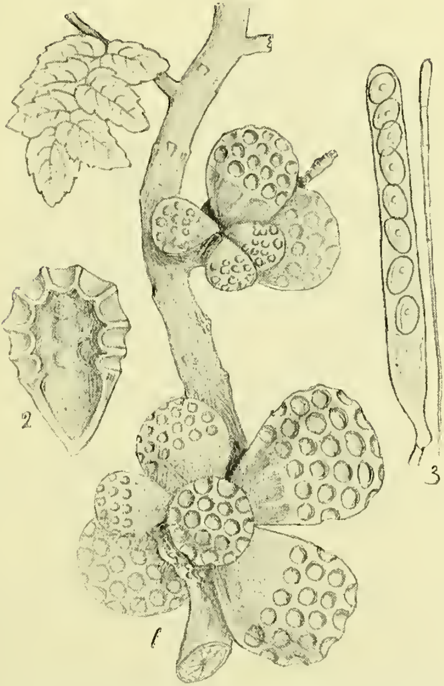

FIG. 79.—*Cyttaria gunnii*, an edible fungus parasitic on the evergreen beech in Tasmania. 1, groups of ascophores on living branch; 2, section of an ascophore; 3, ascus containing eight spores: one paraphysis is also present. One quarter nat. size.

Ascophore turbinate, cup-shaped or discoid; gelatinous when growing, hard and horny when dry.

Bulgarieae.

C.—Ascophore more or less rudimentary, minute, immersed in the matrix, waxy, usually light coloured.
Sticteae.

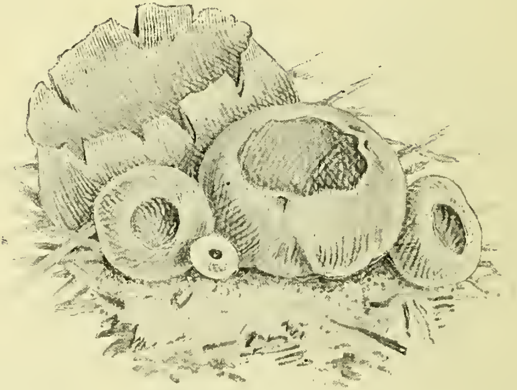

FIG. 80.—*Peziza vesiculosa*, a typical ascigerous fungus belonging to the Discomycetes, which exhibits the peculiarity of puffing out the spores in clouds from the asci. Nat. size.

Ascophore minute, waxy, buried in the matrix, usually blackish, dehiscing through the splitting of the matrix.
Phacideae.

D.—Ascophore superficial, rigid, glabrous, circular, sessile, blackish. Minute, circular, scattered or gregarious.
Patellarieae.

E.—Stroma superficial, erect, branched.

Ascophores cup-shaped, at the tips of the branches of the stroma. *Cordieriteae.*

Cyttarieae

A peculiar family containing only one genus, *Cyttaria.* The general appearance of the ascophore is that of a *Morchella* without a stem. All known species are parasitic on species of evergreen beech (*Fagus*). They often grow in dense clusters, springing from swollen portions of the host. The species are edible, and at one time formed a staple food for the natives.

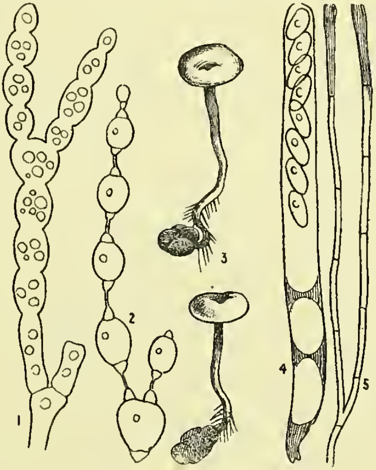

FIG. 81.—*Sclerotinia urnula*, a Discomycete, the conidia of which are liberated by 'disjunctors.' 1, chain of conidia in a young stage; 2, chain of conidia at maturity, the narrow necks or disjunctors deliquesce and liberate the conidia; 3, ascophores springing from mummified berries of *Vaccinium* filled with mycelium, forming a sclerotium; 4, ascus containing eight spores; 5, paraphyses. Fig. 3, nat. size; the remainder highly mag.

Distribution. Chile, Patagonia, Tasmania, and New Zealand.

Helvelleae

Ascophore distinctly stipitate, often large; clavate, conical or subglobose, solid or hollow, sometimes thin and irregularly wavy. Hymenial surface honeycomb-like, brain-like folds, or quite even. Differs from Cyttarieae in having a distinct, elongated stem, and from the stipitate Pezizae in the ascophore not being cup-shaped.

All are saprophytes, mostly growing on the ground, some occur on decayed wood and branches. *Spathularia* and *Mitrula* grow on masses of dead leaves in swampy places, and *Vibrissea* is truly aquatic.

Most abundant in temperate regions.

Pezizeae

Ascophore typically cup-shaped, sometimes becoming almost plane, or even convex, hymenial surface even; sessile or with a distinct, short, or elongated stem. Disc often brightly coloured, due to colouring matter present in the tips of the paraphyses. Variable in size, some exceeding 10 cm. in diameter, others almost microscopic. Many are saprophytic on decaying vegetable matter, others are destructive parasites. Many species produce sclerotia.

Abundant in all countries.

Ascoboleae

The majority of species are minute, some exceedingly so, resembling a minute globule of semi-liquid jelly when seen under a pocket-lens. All species are sessile. In some genera the spores are beautifully coloured, often

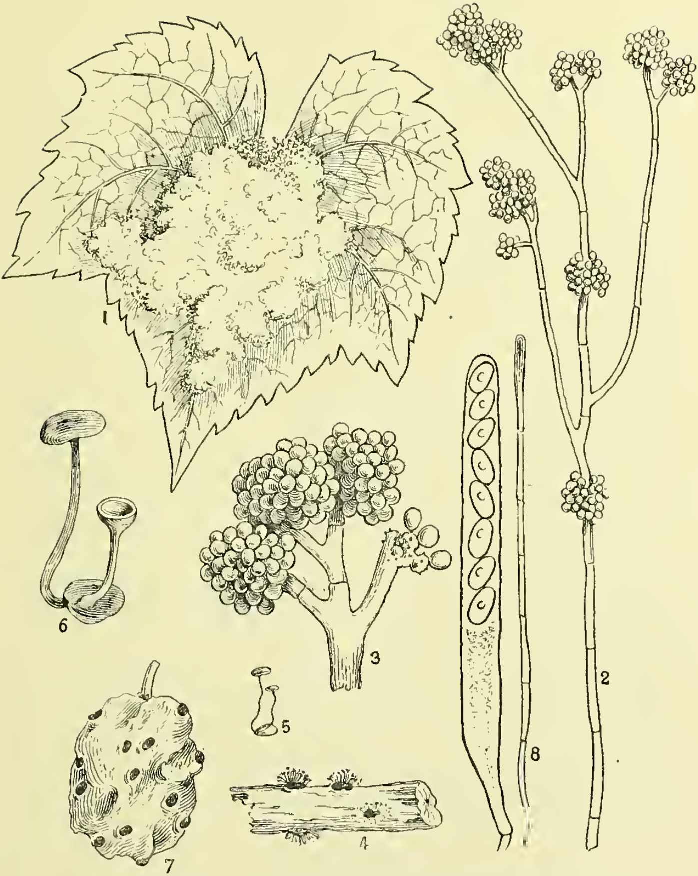

FIG. 82.—*Sclerotinia Fückeliana*, a parasite on the vine. 1, a vine leaf with the conidial (*Botrytis*) stage of the fungus; 2, a conidiophore of the *Botrytis* with clusters of conidia; 3, a head of conidia more highly mag.; 4, small black sclerotia bearing the *Botrytis* form of fruit; 5, a sclerotium bearing two ascophores; 6, the same as fig. 5, mag.; 7, a shrivelled grape with sclerotia embedded in its skin; 8, ascus containing eight spores. Fig. 1, reduced; figs. 4, 5, and 7, nat. size; remainder mag.

commencing pale lilac, and passing through intense violet to opaque brown. In *Ascobolus* the spores are as described above, and when mature show pale streaks or an irregular network of lines on the surface, due to the cracking of the dark epispore, the colourless endospore showing through the cracks. In *Ascobolus* the asci project much above the level of the hymenial surface at maturity, and the spores are ejected elastically in a mass surrounded by gluten, and adhere to whatever they come in contact with. In some species there are numerous spores included in an ascus. In some of the dung-borne species the spores only germinate after passing through the alimentary canal of some herbivorous animal. All are saprophytic.

Species occur everywhere where dung is present.

Dermateae

Usually quite minute. Ascophores often gregarious or crowded and springing from a common, compact base, which is usually immersed in the substratum. Often dry in texture and rather tough; dingy in colour; exterior of ascophore often scurfy or mealy. Generally saprophytic on wood and branches.

Mostly known from temperate regions.

Bulgarieae

Ascophore more or less gelatinous when growing, becoming hard and rigid when dry, and recovering their gelatinous texture when moistened. Often first producing conidiophores. Form variable, discoid, shallowly cup-shaped, or clavate and vertical. Mostly saprophytes.

Distribution general.

Sticteae

Very minute fungi, often appearing as white specks immersed in wood or bark. Ascophore immersed, often at first covered with a white veil, which becomes broken into a fringed, or irregularly torn, reflexed margin at maturity. Excipulum often very rudimentary. Saprophytes.

Generally distributed.

Phacideae

Ascophore minute, more or less immersed in the matrix, urceolate or saucer-shaped when expanded, waxy, excipulum distinct. The matrix is usually blackened and becomes variously ruptured, exposing the disc. Differs from Sticteae in the distinct excipulum, dusky colour, and discoloured matrix. Mostly saprophytes on wood, herbaceous stems, leaves, etc.

Generally distributed.

Cordieriteae

Ascophore rather tough, irregularly branched, more or less erect, apothecia flattened, borne at the tips of the branches. Small, usually reddish in colour; only three or four species known, which are confined to the New World.

Laboulbeniaceae

One of the most remarkable and at the same time most natural of families. Another feature equally remarkable is the fact that our knowledge of this group is, with the exception of some few misinterpreted European species, entirely due to the admirable investigations of one person, Dr. R. Thaxter of Harvard University, U.S.A.

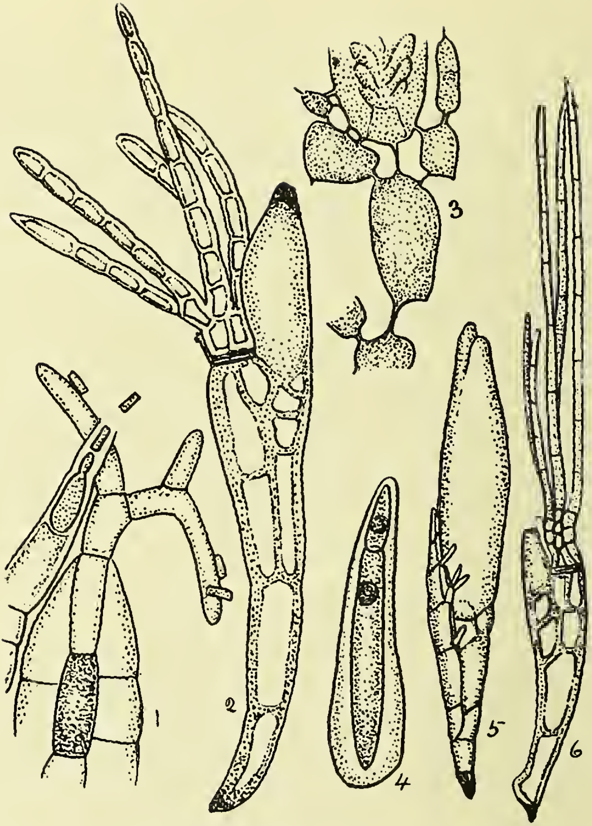

FIG. 83.—1, *Laboulbenia cristata*, young perithecium with antheridia above at the left. The darker axile cell the carpogonium, above it the trichophoric cell terminated by the trichogyne, on which are several antheridia; 2, *Laboulbenia Brachini*, elongate form with exceptionally simple appendages; 3, *Laboulbenia elongata*, portion of a specimen treated with potash and stained with eosin, slightly crushed so as to separate the basal cells without destroying the ascus mass and the inferior supporting cell. The protoplasmic portions of the cells only drawn to show the continuity between adjoining cells; 4, spore of same showing two nuclei; 5, *Sphaleromycetes occidentalis*, mature individual; 6, *Laboulbenia Philonthi*. All highly mag. (After Thaxter.)

All the species are minute, rarely exceeding 1 mm. in length, and the majority are much smaller. Again, all are external parasites on insects with one exception, which occurs on a member of Arachnida. Beetles are the most favoured hosts, especially aquatic forms or those inhabiting damp localities. Some half-dozen species are met with on Dipterous insects, including the common house-fly.

These parasites, unlike the species of *Cordyceps* and other fungi parasitic on insects, appear to cause but little inconvenience to the host, and resemble minute, dark-coloured or yellowish bristles projecting from the chitinous integument, singly, in pairs, or densely crowded and forming a furry coating.

The only known mode of reproduction is of a sexual nature, and has already been described.

The fundamental structure is simple, consisting in many instances of very few cells differently arranged in different genera; in other genera, however, great diversity, often best expressed by eccentricity, is met with in the arrangement of the appendages bearing the male organs.

The ascospores germinate on the host, becoming attacked by a blackened base which serves as an organ of attachment and nutrition. This organ is formed from the lower cell of the two-celled spore. The upper cell of the spore gives origin to the receptacle, which in many simple forms consists of two superposed cells. The upper of these cells gives origin to one or more appendages of very varied form in different genera, and usually bear the antheridia. The female organs are formed from a segment of the lower cell of the receptacle, rarely from the terminal cell. The perithecium, as in many other Ascomycetes, originates from a cell of the receptacle situated below the female organ.

The entire plant is enclosed in a thin, tough, gelatinous envelope. Continuity of protoplasm between the component cells of the entire structure is very marked.

The number of spores in an ascus is either four or eight, hyaline, fusiform or acicular, and with rare exceptions are divided into two cells by a transverse septum. A gelatinous envelope thickened at the base surrounds each spore ; this envelope enables the spore to adhere to its host. When four spores are present in an ascus they are arranged in pairs, and in this manner escape from the perithecium, the asci being previously dissolved. The spores become attached to the host in pairs corresponding to the pairs formed in the ascus, and in dioecious species one spore produces a male and the other a female plant.

The spores germinate on the host, becoming attached by a blackened, modified base which in some species forms a haustorium. New individuals are formed directly by successive cell-division, without forming hyphae.

The present family, though resembling Ascomycetes in producing the spores in a definite number in asci, is not allied in a marked manner to any of the known families belonging to this group. Morphologically, it bears a close resemblance to the Florideae in the structure of the sexual organs, continuity of protoplasm, etc.

The male sexual organs furnish the most important characters on which the classification of the Laboulbeniceae is based. The two primary groups depend on the exogenous or endogenous origin of the antherozoids or male fertilising bodies.

Exogenous antherozoids are produced as lateral branchlets, the whole or portions of which become separated into long, slender rods, having a definite cell - wall.

Endogenously formed antherozoids are differentiated from the protoplasm of an antheridial cell, and eventually escape through a pore at the apex of the cell. A secondary division of the group having endogenously formed antherozoids turns on the simple or compound nature of the antheridium. A simple antheridium is one in which each antheridial cell liberates its antherozoids through its own special pore or opening. In a compound antheridium several antheridial cells are so grouped as to form a specialised organ, and discharge their antherozoids into a common cavity, from which they escape into the surrounding medium through a common pore or opening.

KEY TO THE FAMILIES

Group I.—*Endogenae.* Antherozoids produced endogenously.

Antheridial cells united to form a compound antheridium. Monoecious or dioecious. *Peyritschielleae.*

Antheridial cells distinct, discharging independently. Monoecious or dioecious. *Laboulbenieae.*

Group II.—*Exogenae.* Antherozoids produced exogenously. Typically aquatic.

Antherozoids exogenous. *Zodiomyceteae.*

Peyritschielleae

The principal morphological feature common to this group, in which the antheridia are produced endogenously within specialised cells or groups of cells, consists of the fact that, however closely these specialised antheridial cells may be connected with each other, each cell liberates its contained antherozoids into the surrounding medium through its own proper mouth.

The antheridium usually consists of a flask-shaped cell with a more or less elongated neck, which at maturity becomes perforated at the apex for the discharge of the antherozoids.

Laboulbenieae

In this family the antherozoids are also produced endogenously in more or less flask-shaped antheridial cells; these cells are often six in number, closely compacted together, but instead of being wholly or partly free from each other, both the necks and venters are closely united below, and empty their contents into a common cavity furnished with a neck through which the antherozoids escape.

Zodiomyceteae

In this family, including only two known genera, the antherozoids are produced exogenously. As a rule, the antheridial branches are not highly differentiated, the rod-shaped antherozoids being produced at the tips of branchlets, from which they become separated and adhere to the trichogyne.

The position of this family is not certain; the presence of asci locate it technically in the Ascomycetes.

Berlese, *Laboulbeniaceae*, *Malpighia*, 3, p. 44 (1889).

Burrill and Earle, ‘Parasitic Fungi of Illinois,’ *Bull. Ill. State Lab.*, 2, p. 387 (1887).

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HEMIBASIDIOMYCETES

The members constituting the present Order, so far as known at the time, were originally placed in other existing groups. The Uredineae, along with the Ustilagineae, formed the family known as Hypodermii; the Auricularieae and Tremelleae were included in the Basidiomycetes, whereas the Pilacreae were by some placed in the Hyphomycetes, and by others in the Gastromycetes.

Brefeld first suggested the name Hemibasidii for the Ustilagineae and the Tilletiae, which he considered as representing the connecting-link between the Phycomycetes and the Basidiomycetes. Those Basidiomycetes (Hemibasidiomycetes) with septate basidia he supposed to have descended from the Ustilagineae, whereas the Basidiomycetes with a continuous (not septate) basidium (Auto-

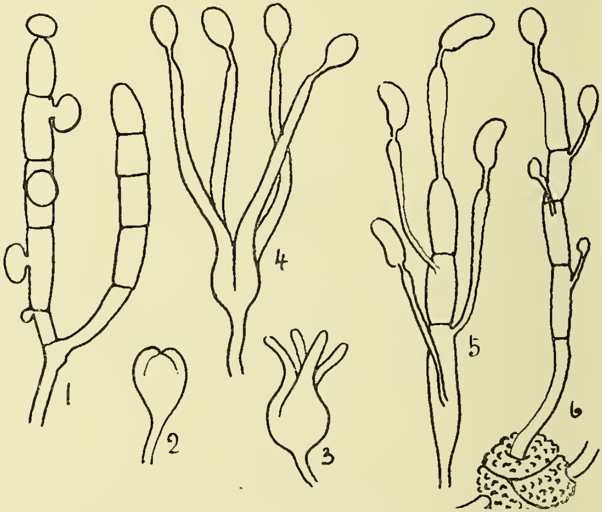

FIG. 84.—Typical basidia of Hemibasidiomycetes. 1, basidium of *Pilacre Petersii*; compare with fig. of basidium of *Tulostoma mammosum*. 2-4, basidia of *Tremella lutescens*, at different ages. 5, basidium of *Exidia auricula-judae*. 6, germinating spore of *Triphragmium ulmariae*: the promycelium or first product of germination is limited in growth and is divided into three or four cells: each cell bears a secondary spore. All highly mag.

basidiomycetes) were considered to have descended from the Tilletiae.

At a later date Möller established a new Order which he called Protobasidiomycetes. This Order included six families, Auricularieae, Uredineae, Pilacreae, Tremelleae, Sirobasidieae, and Hyalorieae. Those families having transversely septate basidia were supposed to spring from *Ustilago*, whereas those with cruciately septate basidia started from *Tilletia*.

Möller does not consider that the Hemibasidiomycetes give origin to the Basidiomycetes proper, an opinion with which I am in agreement. I have previously expressed my view that the Basidiomycetes evolved from conidial forms of the Ascomycetes.

I have followed Möller's arrangement of the Hemibasidiomycetes with the exception of including Ustilagineae (including *Ustilago* and *Tilletia*) in the Order, with which, morphologically, it appears to me to be in closest agreement.

KEY TO THE FAMILIES

Obligate parasites. Spores either formed from the ordinary mycelium or from special branches or sporogenous hyphae, either terminal or intercalary. On germination the spores (chlamydospores or teleutospores) produce a short promycelium; this is either divided transversely by 2-4, usually 3 septae, each cell bearing several secondary spores (*Ustilago*); or the promycelium is continuous (not septate), and bears a cluster of secondary spores at its apex (*Tilletia*). *Ustilagineae.*

Gymnocarpous. Sporophore more or less gelatinous;

basidia transversely septate, 4-spored, differentiated from the substance of the sporophore, and forming a continuous hymenium. *Auricularieae.*

Obligate parasites; often heteroecious. The teleutospores on germination produce a transversely septate basidium (promycelium) which bears four spores. Aecidia and uredospores often present. *Uredineae.*

Angiocarpous. Sporophore subglobose, supported on a slender stem; basidia transversely septate, bearing four spores. *Pilacreae.*

Basidia with septa arranged obliquely to the long axis, produced in chains. *Sirobasidieae.*

Angiocarpous. Sporophore more or less gelatinous; basidia divided by two septa crossing at right angles, each cell growing out into a long sterigma and bearing a spore at its apex. *Tremelleae.*

Basidia as in Tremellaceae, but the fruit is angiocarpous. *Hyalorieae.*

Ustilagineae

All the members of the present group are parasites, mostly met with in the aerial portions of flowering plants, although some few develop in mosses, hepatics, etc. In many instances the spores are produced in the ovary of the host, where they often form a black pulverulent mass when mature, as in the 'smut' or 'bunt' of oats and wheat. In some instances the spores are formed in the anthers, in others on the leaves, whereas in the case of maize or Indian corn, the smut often forms irregular

FIG. 85.—*Urocystis occulta*, one of the Ustilaginaceae. 1, upper part of a rye plant attacked by the fungus; 2, clusters of spores, one of which has germinated and produced a cluster of secondary spores; 3, a spore that has germinated and produced secondary spores, two of which have germinated, *a*. Fig. 1, reduced; the others mag.

swellings that may attain to the size of an apple, and occur either on the stem, leaves, or fruit.

In some instances infection of the host-plant is only possible during a very short period after germination; the mycelium of the fungus grows along with the host without doing any apparent injury until the spores are formed in the ovary or on the leaves. In the case of maize, however, infection can occur at any period of growth provided quite young tissue is present.

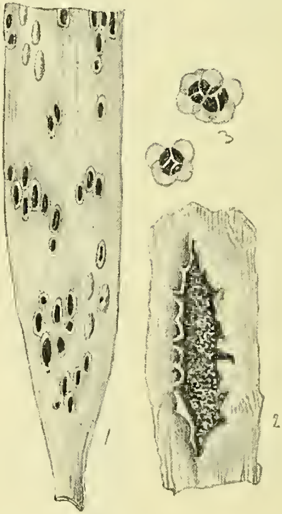

FIG. 86.—*Urocystis colchici.* 1, portion of a leaf of *Colchicum autumnale* with numerous sori of teleutospores; 2, a single sorus bursting through the epidermis of the leaf; 3, spores, showing the central living cells surrounded by empty sterile ones. Fig. 1, nat. size; fig. 2, slightly mag.; fig. 3, highly mag.

In other instances infection occurs in the flower, the spores being deposited by some agent on the stigma, and a mycelium is formed in the ovary. The mycelium is very delicate, septate, widely diffused in the tissues of the host, mostly intercellular. Haustoria are produced by some species. The resting-spores—teleutospores of some—are either formed from the ordinary mycelium or from specialised branches, and are either naked as in *Ustilago*, or contained in a special receptacle as in *Sphacelotheca*. In the genus *Entyloma* spores are formed on all parts of the mycelium, their first indication being the appearance of spherical swellings which continue to increase for some time, and may be either terminal or intercalary. From the protoplasm in these swellings the spores are formed, and form their own cell-wall while yet enclosed in the wall of the hypha. The wall of the hypha forms a gelatinous outer coating to the spore in some species. In *Ustilago* the spores are formed on special branches or sporogenous hyphae, which are very much branched and produced in great numbers at definite points in the tissue of the host. These sporogenous hyphae become cut up into isodiametric portions by transverse septa; at the same time the wall swells very much, forming a gelatinous membrane enclosing the protoplasm, which develops into a spore provided with its own cell-wall, while yet enclosed in the gelatinous wall of the hypha, which eventually disappears, leaving the spores as a dry, dusty mass. In the genera *Sorosporium*, *Tubercinia*, and *Urocystis* the spores are produced in compact clusters, and surrounded by a special envelope which either soon disappears, or is persistent. In *Urocystis* this envelope consists of sterile cells. A glimpse of the highly specialised peridia containing the spores in some forms of the

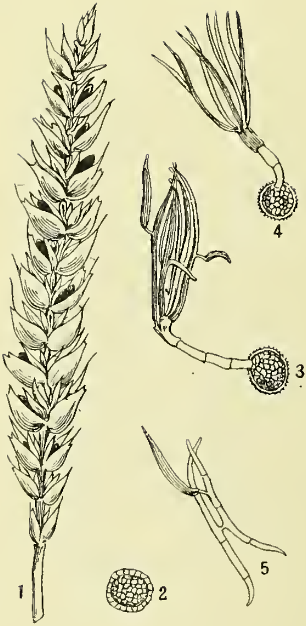

FIG. 87.—*Tilletia caries*, a species parasitic on wheat. 1, ear of wheat diseased; 2, spore; 3, 4, spores germinating and producing a germ-tube bearing a cluster of secondary spores at the tip; 5, two secondary spores that have conjugated or become united by a thin transverse tube: one of the secondary spores has produced a conidium. (Figs. 3-5 after Brefeld.) Fig. 1, nat. size; remainder highly mag.

Uredinaceae, are seen in *Doassansia*, where the clusters of spores are enclosed in a peridium of closely packed, dark coloured, sterile cells arranged in a single layer. In *Sphacelotheca hydropiperis*, which invests the ovary of *Polygonum hydropiper*, the sporophore is more complex, being furnished with a thick outer wall and a central axis or columella, the spores being produced in the cavity between the two. The spores described above are resting-spores, or chlamydospores of Brefeld, germinating after a period of rest. Aecidia are unknown. Conidia are present in the genera *Entyloma* and *Tubercinia*, appearing as delicate white mould-like patches on the living leaves of the host-plant.

The first product of germination of a resting-spore is a germ-tube of limited growth, the promycelium, which soon bears small secondary spores. A remarkable feature about these secondary spores is that they usually conjugate in pairs; that is, adjacent pairs become organically connected by a short tube growing from one and fusing with the other. In some instances, as in *Tilletia*, this fusing occurs before the secondary spores break away from their point of origin. After conjugation a slender germ-tube is formed which receives the protoplasm from both secondary spores, and if situated on a suitable host, penetrates the tissue and forms a mycelium. In some species the germ-tubes arising from the conjugation of two secondary spores produce tertiary spores; these in turn produce germ-tubes capable of infection. The above mode of germination occurs when resting-spores germinate in water, but Brefeld has shown that when placed in a nutrient solution the results are quite different. Instead of giving origin to a promycelium of limited length, the germ-tube continues to grow

FIG. 88—*Ustilago avenae*, a parasite on oats. 1, a 'smutted' ear of oats; 2, spores; 3, germinating spores: numerous secondary spores are produced by each cell of the promycelium: these secondary spores reproduce themselves rapidly by budding, as in yeasts, and frequently form simple or branched chains before they separate from the promycelium; 4, secondary spores conjugating in pairs. Fig. 1, reduced; the remainder highly mag.

into a dense branched mycelium which eventually bears secondary spores, either in the liquid or on branches that rise into the air; or the mycelium continues to develop like the sprouting fungi by gemmation or the production of myriads of minute cells, which become detached as in the yeasts or Saccharomycetes.

De Bary considered the conjugation of secondary spores as a sexual act, an idea not now entertained; furthermore, there is no evidence of sexuality met with in the group.

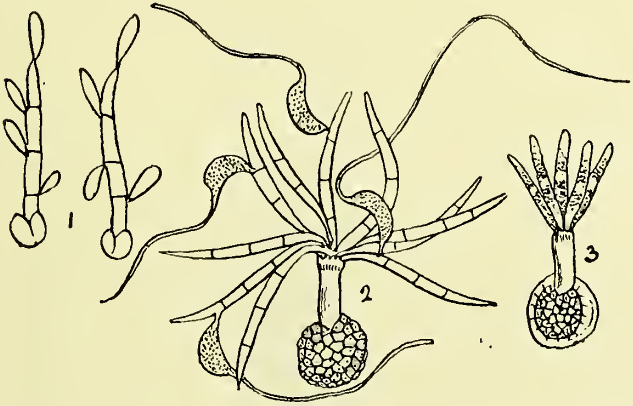

FIG. 89.—Germinating spores of species of Ustilaginaceae. 1, *Ustilago arundinellae*; 2, *Tilletia decipiens*, the secondary spores producing tertiary spores; 3, *Tilletia zonata*. (After Brefeld.) All highly mag.

Two distinct types of structure are manifested in the mode of germination of resting-spores. In the first, illustrated by *Ustilago*, the short promycelial tube is divided into three or four cells by transverse septa, and each cell gives origin to one or several secondary spores. Those species having this type of structure are considered by Brefeld as being the progenitors of the group he terms Hemibasidiomycetes, where the basidium is transversely septate. In the second type, represented by *Tilletia*, the promycelium is short and not divided by septa, but bears a variable number of secondary spores at its apex. The

FIG. 90.—*Ustilago hordei*, a species parasitic on barley. The mass of spores does not become loose and powdery at maturity as in most species of *Ustilago*. Nat. size.

Basidiomycetes, where the basidium is not cut up by septa, but one-celled, and bearing spores at its apex, is considered by Brefeld as having originated from this second type.

Representatives of the group are widely distributed, being met with practically everywhere where suitable host-plants grow. In many instances a perennial mycelium is present in the root or stem of the host-plant.

Auricularieae

Gelatinous, becoming rigid when dry. Hymenium distinctly inferior, vaguely costate or plicate. Upper sterile surface strigose or minutely downy. The habit is that of certain species of *Stereum*. Differs from Tremellaceae in the transversely septate basidia.

Hirneola polytricha, a species widely distributed in the tropics and southern hemisphere, is much esteemed as an article of food by the Chinese. The British species, *Hirneola auricula-judae*, is a typical representative of the group.

Widely distributed.

Sirobasidieae

Forming minute gelatinous masses completely surrounded by the hymenium. The principal feature consists in the basidia being produced in chains, the terminal basidium being the oldest. Each basidium, or interstitial swollen portion, is divided by septa into two or four cells; each cell bears a single spore. Occupying an intermediate position between Pilacraceae and Tremellaceae.

Only three species known. All from S. America.

Uredineae

Obligate parasites on higher plants, developing most frequently on the leaves, but often occurring on all growing parts of the plant, and in many instances causing considerable distortion of the part attacked. The mycelium is intercellular, giving off certain branches or haustoria, which enter the cells for the purpose of obtaining food. In many species the mycelium is localised or confined to a limited area. After infection the mycelium produced extends for a limited distance centrifugally, hence in many species the particular form of fruit produced is arranged in

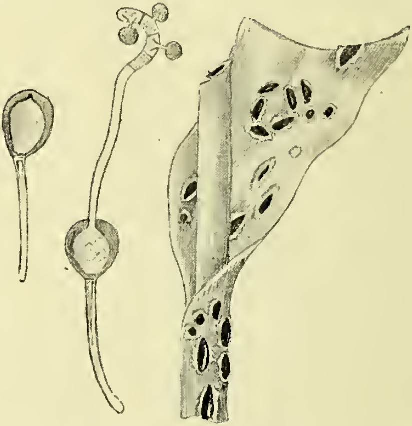

FIG. 91.—*Uromyces colchici.* 1, portion of a diseased *Colchicum* leaf: the sori are sometimes arranged in irregular circles; 2, two teleutospores, showing the single germ-pore at the apex: one has germinated and produced a promycelium tube bearing three secondary spores near the apex. Fig. 1, nat. size; remainder highly mag.

more or less perfect concentric circles, as in *Aecidium zonale*, *Uromyces scillarum*, *U. colchici*, *Puccinia lychnidearum*, etc. In many instances this centrifugal manner of growth is interfered with by the special structure of the portion of the host-plant infected. When the venation of a leaf is strongly pronounced, the centrifugal method of extension is much modified, and in many instances completely neutralised. This is especially marked in the case of Uredines developed on the leaves of grasses and sedges, where, owing to the presence of strongly developed parallel rows of vascular bundles or veins, the sori or spore masses are always elongated or linear in form, as in *Puccinia graminis*, *P. rubigo-vera*, etc.

On the other hand, the mycelium is in some species by no means localised, but permeates almost every part of the host. Such mycelium is generally perennial, and consequently when a plant is once infected it remains so during the remainder of its life. As illustrations of such perennial mycelium may be mentioned the teleutospore form of species of *Gymnosporangium*, produced on various species of juniper; *Endophyllum euphorbiae*, *Aecidium leucospermum*, *A. punctatum*, *A. tragopogonis*, etc.

Heteroecism, as already stated, is common in the Uredineae, and this phenomenon implies the presence of more than one form of spore produced by the same species during different periods of its life-cycle. Five such spore-forms are known to exist, but it is very unusual for all the five forms to be produced by any given species. The spore-forms, always produced in the following sequence, are as follows: Spermatia, Aecidiospores, Uredospores, Amphispores, Teleutospores.

The spermogonia or conceptacles containing the sper-

FIG. 92.—*Gymnosporangium clavariaeforme.* 1, teleutospore stage of the fungus parasitic on a juniper branch: the mycelium is perennial in the branch, which becomes swollen or spindle-shaped; 2, two teleutospores supported on very long pendicles or stalks: the red gelatinous masses produced on the juniper branch consist entirely of teleutospores; 3, teleutospores germinating and producing secondary spores; 4, aecidium stage on a pear leaf; 5, aecidium stage on branch, leaves, and fruit of hawthorn; 6, aecidiospore germinating: the promycelium bears four secondary spores near the tip. Figs. 1, 4, and 5, nearly nat. size; the other highly mag.

matia are minute, subglobose, or flask-shaped structures, either immersed in the epidermis, or only covered by the cuticle, through which the open neck protrudes. The spermatia, produced at the tips of delicate hyphae springing from the basal portion of the inner surface of the spermogonium, are very minute, hyaline, and one-celled. The significance of spermogonia and spermatia is not clearly understood. In certain instances spermatia have been induced to germinate. Cornu did this by placing the spermatia in a weak solution of sugar in water. Notwithstanding such power of germination, spermatia appear to be quite incapable of producing a mycelium, or of giving origin to a new phase of the fungus. The most general opinion respecting spermatia is that which regards them as effete male organs, equivalent to the organs present in *Collema* and other Lichens. If this view is correct, it implies the presence at some past period of a trichogyne, a view advocated by Blackman, as already described. In many species the production of spermogonia has completely ceased, but when present they always accompany the aecidium stage.

The aecidiospores are produced in chains within a special structure called an aecidium or pseudoperidium. Aecidia are popularly known as 'cluster-cups.' When the peridium is short and opens in a stellate manner with the lobes recurved, it once constituted the genus *Aecidium*. When the peridium is long and cylindrical, it constituted the old genus *Roestelia*. The aecidiospores are one-celled, with a colourless cell-wall, and usually bright orange contents. The pseudoperidium sometimes opens by a pore, but more frequently becomes torn irregularly at the apex; the torn edge splits at intervals, and the segments become reflexed, thus exposing the contained mass of spores. The wall of the pseudoperidium is formed in the same fashion as the chains of spores in its interior, only the cells are sterile and empty. Aecidiospores have several germ-pores, or specialised portions of the epispore, through which the germ-tubes protrude on germination. If a germinating aecidiospore happens to be situated on the leaf or other suitable portion of the proper host-plant, the germ-tubes pass through the stomata into the living tissues below the epidermis, where a mycelium is formed which in due course

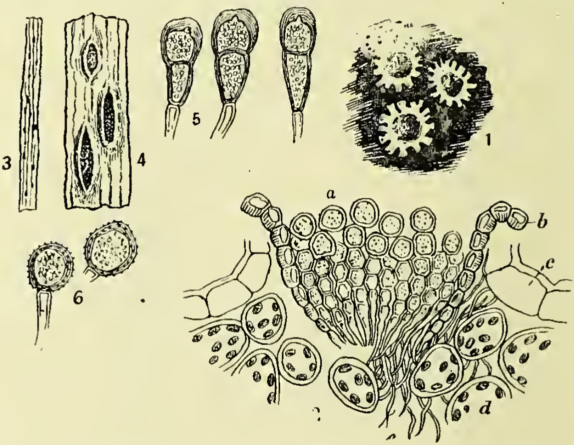

FIG. 93.—*Puccinia pringsheimiana*, a parasite on gooseberry leaves. 1, portion of a gooseberry leaf with three aecidia or 'cluster-cups' fully expanded; 2, section through an aecidium, showing at *a* the spores produced in chains, which soon break up and form an orange, powdery mass; *b*, the protective wall or peridium; *c*, epidermal cells of the leaf; *d*, the parenchymatous cells of the leaf containing chlorophyll: the mycelium of the fungus is shown running between the cells of the leaf; 3, portion of leaf of a sedge bearing the sori or minute clusters of uredospores and teleutospores; 4, same as fig. 3, more enlarged; 5, teleutospores; 6, uredospores. Fig. 3, nat. size; remainder mag.

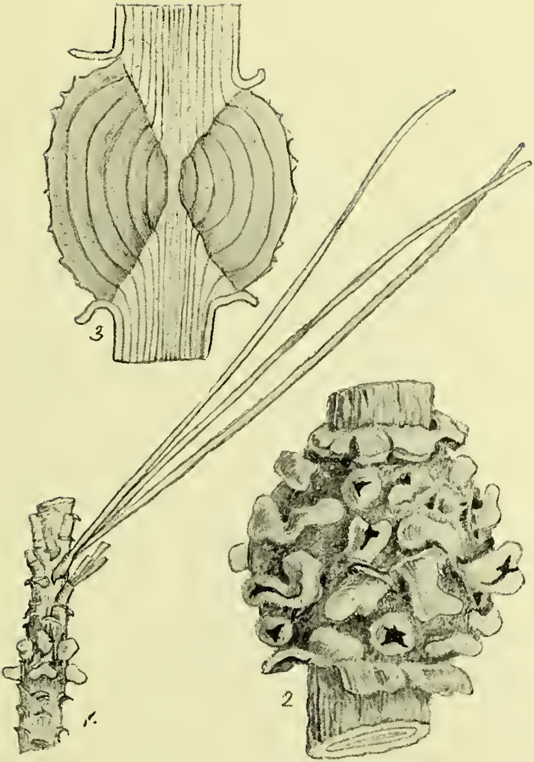

FIG. 94.—*Peridermium harknessi*, a destructive parasite on various conifers in the United States. 1, portion of the stem of a seedling three years old, of *Pinus ponderosa*, showing the aecidia of the *Peridermium* bursting through the bark; 2, appearance of portion of a stem of the same species of host, eight years old, attacked by the fungus, the swollen portion being thickly covered with aecidia that have burst through the bark; 3, section through fig. 2: the shaded portion indicates the number of annual rings of wood that have been stimulated to excessive growth by the mycelium of the fungus. All the figs. slightly reduced.

gives origin to the next cycle of development, which is usually the uredospore condition.

Uredospores may be produced from mycelium produced from aecidiospores; this is the usual mode by which uredospores are first produced in the spring. During the summer one crop of uredospores follows another in quick succession without the intervention of any other form of spore. Uredospores may also be produced by the mycelium originating from the germination of promycelium spores or secondary spores. In many instances uredospores germinate at the moment of maturity, and only retain their vitality for a short period of time. In some species, however, as *Puccinia graminis*, *P. rubigo-vera*, etc., the uredospores retain their vitality through the winter, and are capable of infecting a proper host-plant the following season. Uredospores are one-celled, have from two to

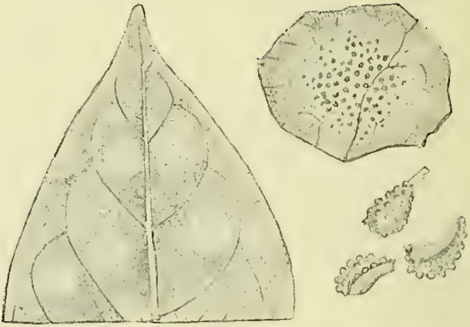

FIG. 95.—*Hemileia vastatrix*, a parasite causing the well-known coffee leaf disease. 1, portion of a coffee leaf showing diseased patches; 2, portion of a leaf showing a group of sori; 3, uredospores. Figs. 1 and 2, nat. size; fig. 3, highly mag.

twelve germ-pores, and are produced singly at the tips of unbranched hyphae; these hyphae are produced in dense clusters just below the epidermis, which is finally ruptured, exposing the sorus or dense aggregation of uredospores.

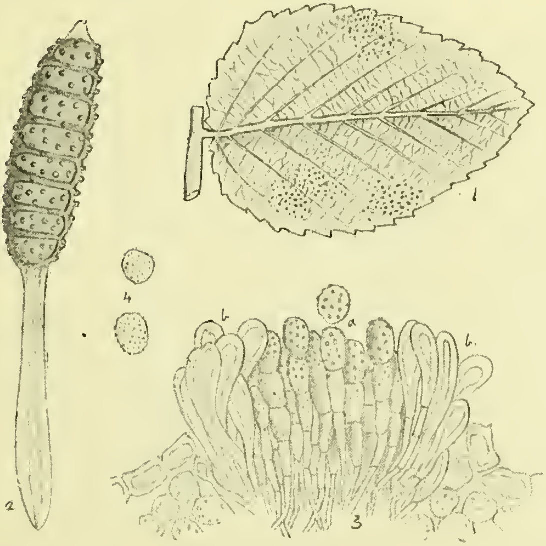

FIG. 96.—*Phragmidium rubi-idaei*, a parasite on raspberry leaves. 1, under surface of a raspberry leaflet showing numerous sori of teleutospores; 2, teleutospore; 3, section through an aecidium; *a*, chains of spores; *b*, *b*, large sterile cells or paraphyses forming the covering of the aecidiospores; 4, uredospores. Fig. 1, nat size; remainder mag.

The sori of uredospores become exposed in all known instances, excepting the genus *Hemileia*, by rupturing the epidermis. In *Hemileia* the hyphae bearing the uredospores—and later the teleutospores—emerge in small clusters through the stomata.

Amphispores, like uredospores, are one-celled, and have several germ-pores, but the cell-wall is thicker, and as in teleutospores, germination is delayed until after a period of rest. This form of spore is known in only a few species, mostly N. American forms. Amphispores are perhaps most abundant in the widely distributed *Puccinia pruni*.

Teleutospores, as the name implies, are formed last in the sequence of spore-forms enumerated, although in some species teleutospores alone are produced, as in *Puccinia malvacearum*. Teleutospores vary considerably in structure and number of component cells in different genera. In *Uromyces* the teleutospore is one-celled, with a single germ-pore at the apex; in *Puccinia*, two-celled; in *Triphragmium*, three-celled; whereas in *Phragmidium* and *Xenodochus*, the teleutospore consists of a chain of cells. The one distinguishing constant feature of a teleutospore is the immediate product of germination. This consists of a promycelium tube of limited growth, which becomes four-celled by the formation of transverse septa; each cell then bears a single secondary spore, promycelium spore, or sporidium, as it has been variously named. On the other hand, aecidiospores, uredospores, and amphispores on germination produce ordinary vegetative hyphae, which directly form mycelium. Teleutospores form sori which rupture the epidermis, and are produced singly at the tips of unbranched hyphae, except in the genus *Uromycladium*, recently founded by M'Alpine, where the hyphae bearing teleutospores are branched near the apex.

Teleutospores, also called winter spores or resting-spores, usually only germinate after a period of rest, and the secondary spores produced give origin to the mycelium from which the aecidial phase of the fungus originates the following season. In *Puccinia malvacearum* and other allied species where teleutospores alone are produced, the teleutospores germinate at the moment of maturity, and before they fall from the sorus; the secondary spores formed infect other plants throughout the season after the manner of uredospores in other species.

FIG. 97.—*Phragmidium subcorticatum*, a common parasite on rose-trees. 1, rose branch and leaves, infected with the aecidium stage of the disease, which forms deep orange, powdery masses; 2, leaf with numerous sori of teleutospores; 3, teleutospores; 4, uredospores. Figs. 1 and 2, nearly nat. size; remainder highly mag.

Perhaps nowhere else in the whole range of fungi has such extreme differentiation, both morphological and physiological, taken place as in the genus *Puccinia*, expressed by such terms as heteroecism, biological forms,

FIG. 98.—*Melampsora pinitorqua*, a fungus whose aecidiospores are produced in chains. 1, top of a young pine attacked by the aecidial form of the fungus; 2, three chains of aecidiospores in different stages of development; 3, an aspen leaf with pustules formed by the teleutospore stage of the fungus; 4, section through a pustule or sorus of teleutospores, as yet covered by the epidermis of the leaf. Figs. 1 and 3, rather less than nat. size; the remainder mag.

bridging forms, etc. The following arrangement of the species in the genus *Puccinia*, taken from Saccardo, illustrates the gradual elimination or dropping out of the various spore-forms.

Puccinia

Sect. A. **Eu-Puccinia.**—Spermogonia, aecidia, uredospores and teleutospores produced on a living host; teleutospores germinating after a period of rest (not on a living matrix).

I. **Auto-Puccinia.** — Spermogonia, aecidia, uredo- and teleutospores produced on the same matrix.

Ex. *Puccinia galii*, on various species of *Galium*.

II. **Hetero-Puccinia.**—Secondary spores germinating and giving origin to aecidia on a different species of host-plant to that on which the teleutospores were produced.

Ex. *Puccinia graminis*, aecidia on Barberry, remainder on wheat.

Sect. B. **Brachypuccinia.** — Spermogonia, uredo- and teleutospores produced on the same matrix; aecidia absent.

Ex. *Puccinia suaveolens*, on thistle (*Cirsium*).

Sect. C. **Hemipuccinia.**—Uredo- and teleutospores produced on the same matrix; spermogonia and aecidia absent.

Ex. *Puccinia polygoni*, on various species of *Polygonum*.

Sect. D. **Pucciniopsis.**—Spermogonia, aecidia and teleutospores produced on the same matrix; uredospores absent (or rarely a few mixed with the teleutospores).

Ex. *Puccinia tragopogonis*, on goat's-beard (*Tragopogon*).

Sect. E. **Micropuccinia.**—Teleutospores only produced; germinating only after a long period of rest on the dead matrix.

Ex. *Puccinia ribis*, on currant and gooseberry.

Sect. F. **Leptopuccinia.**—Teleutospores only produced; germinating at once on the living host-plant.

Ex. *Puccinia malvacearum*, on hollyhock and various mallows.

Many of the most destructive parasites known are members of the present family. Distribution cosmopolitan.

Pilacreae

This family is represented by one genus only, *Pilacre*, which includes under twenty species scattered throughout the world. The habit and general appearance is similar in all; the plants rarely reach half an inch in length, and resemble a miniature drumstick with a stout stalk, or they may be compared to *Lycoperdon gemmatum* in miniature. Two species are met with in this country, but are decidedly rare, having hardly been recorded outside Epping Forest, where they are not uncommon, growing in dense clusters on trunks of hornbeam.

The genus was considered as belonging to the Hyphomycetaceae or moulds, and to approach in structure such genera as *Stilbum* and *Graphium*, until Brefeld pointed out that the spores were produced on specialised, short, transversely septate hyphae; about three septa are present dividing the protobasidium into four cells, each of which bears a sessile, coloured spore. On account of this structure, Brefeld placed *Pilacre* in the Protobasidiomycetes.

A vertical section of a species of *Pilacre* resembles superficially that of a typical *Lycoperdon*, although there is no near affinity between the two.

The stem is solid, and expands at the apex into a more or less globose head or columella, from which the fertile hyphae originate. These hyphae are densely crowded and radiate in every direction, forming a globose head. Each hypha gives off at different levels short lateral branches which bear clusters of protobasidia. Each hypha runs out into a sterile terminal portion furnished with variously coiled and contorted branches. These sterile tips become more or less interwoven and linked together by their spiral branches, and collectively form a kind of external protective covering or peridium, which encloses the central spore-producing mass of hyphae. The fruit is thus said to be angiocarpous.

Tremelleae

The species are soft and gelatinous when moist, becoming rigid and horny when dry, but again becoming gelatinous when moistened. According to Brefeld and others, the basidia are longitudinally divided by two septa crossing each other at right angles. I am not convinced that this is the true explanation of the appearance presented by the basidia. When quite young the basidium appears as a smooth, broadly obovate body terminating a slender hypha. As it increases in size, when viewed from above, two very slight depressions crossing at right angles are visible on its upper surface. The four portions of the apex of the basidium, defined by the depressions crossing each other, respectively grow out into a basidium, stoutest

FIG. 99.—*Tremella frondosa*. Half nat. size. (After A. Clarke.)

at the base. I have never been able to find a septum, in the sense of a plate penetrating the substance of the apex of the basidium, but consider the cross marking present at the apex of the basidium as simply due to the first bulging out of the stout bases of the four sterigmata. If this idea proves to be correct, the Tremellaceae must return to the Basidiomycetes proper and occupy a position next to Dacryomycetaceae. Many of the species are large, composed of brain-like convolutions, and sometimes brightly coloured. In some species of *Tremella* large numbers of conidia are produced in the substance of the sporophore, below the hymenium. In *Tremellodon* the sporophore is more or less tongue-shaped, growing horizontally, and furnished on the under surface—the hymenium—with crowded spines, as in the genus *Hydnum*.

Brefeld has shown that the spores of many species, on germination, produce secondary spores almost at once.

Saprophytes, growing on wood.

Widely distributed.

Hyalorieae

The basidia are of the same type as in Tremellaceae, but the present family differs in the stiptate, erect sporophore which is thickened at the apex, and is parallel with the Pilacreaceae in general build, but is gymnocarpous.

One species known, from Brazil.

Arthur, 'Amphispores of the Grass and Sedge Rusts,' *Bull. Tor. Bot. Club*, 32, p. 35 (1905).

Brefeld, 'Protobasidiomyceten,' *Unters. Ges. Mykol.*, 7. Heft (1888).

Brefeld, 'Brandpilze [Ustilagineae],' *Unters. Ges. Mykol.*, 5. Heft (1883), 11. Heft (1895), 13. Heft (1905).

Clinton, 'Mon. N. American Ustilagineae,' *Proc. Boston Soc. Nat. Hist.*, 39, p. 320 (1904).

Engler and Prantl, *Hemibasidii* [*Ustilagineae and Tilletieae*], 1, pt. 1** (1900).

Holway, 'N. American Uredineae' (1905).

Massee, 'Ustilagineae (British),' *Brit. Fungi* (1895).

Massee, 'A Revision of the Genus *Tilletia*,' *Kew Bull.* 1899, p. 141.

Massee, 'Spore Variation in the Genus *Triphragmium*, etc.,' Grevillea. 21, p. 113.

M'Alpine, 'A New Genus of Uredineae—*Uromycladium*,' *Ann. Mycol.*, 3, p. 303 (1905).

Möller, 'Protobasidiomyceten,' *Bot. Mittheil. aus den Tropen*, A. W. Schimper, 8. Heft (1895).

Plowright, *Mon. Brit. Uredineae and Ustilagineae*, London (1889).

Saccardo, *Uredineae and Ustilagineae*, 7, pt. 2 (1888).

Sydow, *Monographia Uredinearum* (1894).

BASIDIOMYCETES

The enormous assemblage of species included in the present group possess only one common morphological bond of union, namely, the basidium on which the spores are borne. A basidium consists of a comparatively large, usually more or less clavate cell, from the free apex of which spring four, less frequently two, slender outgrowths or sterigmata; each sterigma bears a spore. In the Dacryomycetaceae the spores are generally septate, elsewhere throughout the entire group the spores are one-celled. No trace of sexual reproduction is known unless Dangeard's view is accepted.

FIG. 100.—Typical forms of basidia in the Basidiomycetes. 1, basidia and spores of *Tulostoma mammosum*: the basidia are elongated, and the spores grow along its length as in the Hemibasidiomycetes, but the basidium is not septate; 2, bisporous basidium of *Dacryomyces deliquescens*. 3, basidia and fusiform cystidia having the upper portion covered with particles of oxalate of lime, of *Peniophora inconspicua*. 4, bisporous basidia of *Lycoperdon echinatum*. 5, two spores of same showing the persistent sterigmata. 6, tetrasporous basidia with sessile spores, of *Scleroderma vulgare*. 7, portion of hymenium of a typical agaric, *Inocybe asterospora*, showing tetrasporous basidia; paraphyses, somewhat smaller than the basidia, and not bearing sterigmata; cystidia, longer than the basidia. In many species of *Inocybe*, like the present one, the cystidia, when mature, are crowned by an amorphous mass, resembling a cluster of dark-coloured crystals. This is caused by the exudation and hardening of the contents of the cystidium. 8, free spore of No. 7. All highly mag.

Many species have conidial forms of reproduction.

Distinguished from Hemibasidiomycetes by the basidia being one-celled.

KEY TO THE SUB-ORDERS

Hymenium naked and exposed from the first, or at all events before the spores are mature. *Hymenomycetes.*

Hymenium enclosed in a special covering until the spores are mature. *Gasteromycetes.*

HYMENOMYCETES

The principal feature of this group consists in the hymenium or spore-bearing surface being exposed from the first, or at all events before the spores are mature. Two leading ideas are persistently kept in view during the evolution of the group. One of these is the production of the greatest area of spore-bearing surface with the least expenditure of material. The other idea is concerned with the protection of the hymenium from injury, whether due to climatic conditions or the attacks of animals. The gradual progress of these ideas is followed in detail in treating of the respective families forming the Hymenomycetes, and it is sufficient at present to state that both ideas are most perfect in the highest and newest group, Polyporeae, where the hymenium is protected against adverse weather in the interior of hollow tubes, and against the attacks of living enemies by the indurated consistency of the sporophore, which in the highest species is hard and woody. This comparative perfection has led, for the first time since the differentiation of the fungi as a group, to the appearance of perennial forms.

There are no obvious departures from the type ideas of structure presented by the Polyporeae, that suggest the evolution of another sub-family.

In the genus *Nyctalis* chlamydospores are formed on the surface of the pileus. Conidia are formed in certain species of *Polyporus* and *Fistulina*, and oidia are known in some agarics.

KEY TO THE FAMILIES

Sporophore gelatinous; basidia with two long, stout sterigmata. *Dacryomyceteae.*

Sporophore erect, club-shaped or much branched, everywhere covered by the hymenium. *Clavarieae.*

Sporophore resupinate, dimidiate or with a central stem; hymenium even, confined to one side of the sporophore. *Thelephoreae.*

Sporophore resupinate, dimidiate or with a central stem; hymenium borne on spine-like processes. *Hydneae.*

Sporophore resupinate, dimidiate or with a central stem; hymenium borne on flat plates or gills. *Agaricineae.*

Sporophore resupinate, dimidiate or with a central stem; hymenium on the inner surface of tubes or shallow depressions. *Polyporeae.*

Dacryomyceteae

Gelatinous when moist, horny when dry. Always small, appearing as small spots of orange or dingy yellow jelly on dead wood in *Dacryomyces*; as more or less fan-shaped, erect plates in *Guepinia*, common in the tropics; or as erect, simple, or branched structures resembling a *Clavaria*, in *Calocera*.

Distinguished by the gelatinous consistency and basidia with two long, stout sterigmata. In most species the spores are septate, or become so during germination. Septate spores are unknown elsewhere in the Basidiomycetes.

Generally distributed.

Clavarieae

The members of this family present great variety of form; the most primitive types consisting of a simple, upright, more or less clavate or club-shaped sporophore, hence the name of the family. On the other hand, the most highly differentiated genus, *Sparassis*, consists of a dense mass of contorted tissue that has been compared in appearance to the heart of a cauliflower, which it approaches or sometimes exceeds in size. Between these two extremes there is almost every conceivable form, commencing with a very slightly branched sporophore, as in *Clavaria rugosa*, and passing on to such types as *C. abietina*, etc., where, from a short stem, spring many short, main branches, which, by repeated dichotomous divisions, forms a densely branched head. The ultimate branchlets are often forcipate, or curved inwards towards each other, and the axils are often conspicuously rounded or lunate. Some of the minute forms spring from a small sclerotium.

The general scheme of structure throughout the group is primitive, the whole surface of the sporophore is fertile, and there is no protection, structural or physiological, for the hymenium against climatic influences or living enemies.

The one observable line of evolution is in the direction of gaining a greater spore-bearing surface or hymenium by the rearrangement of an equal amount of material. This idea is illustrated by comparing *Clavaria pistillaris* with *C. formosa*. The former has a solid, undivided, typically club-shaped, erect sporophore, ten to fifteen cm. high, and two to three cm. diameter at the thickest part. The entire surface of the sporophore is covered with the hymenium. In *C. formosa*, the gross weight of which does not exceed that of *C. pistillaris*, from a stout, very short, solid base spring numerous slender, closely compacted branches and branchlets, each completely covered with the hymenium,

FIG. 101.—*Clavaria fastigiata.* A saprophytic fungus growing on the ground among grass, and obtaining its food from humus. Nat. size.

the whole collectively affording a very much greater spore-bearing surface than that present in *C. pistillaris*.

Notwithstanding this line of development, which is so pronounced within the family, it is not continued and extended in succeeding families, but dies out with the Clavariaceae, which for this reason must be considered as a terminal group. It was an idea mooted at the commencement of the Basidiomycetes, which for some unknown reason was early abandoned.

Bisporous and tetrasporous basidia respectively occur constantly in different species belonging to the same genus. Cystidia are sometimes present. All the species are edible; the absence of differentiated poisonous products, so common in the higher Basidiomycetes, is in itself evidence of a primitive position in the order of evolution of the families composing the Basidiomycetes.

The spores range in colour in different species from perfectly colourless, through various suggestions of yellow up to deep ochraceous, when seen in the mass thrown down on paper.

The majority grow on the ground; a few of the smaller kinds are met with on dead herbaceous stems or amongst decaying vegetable matter.

There are no true parasites.

The family is best represented in temperate regions.

Certain members of the Thelephoraceae resemble species of *Clavaria* and *Pterula* superficially, and one genus of the last-named family called *Lachnocladium* has been included in the Clavariaceae by Saccardo in his *Sylloge Fungorum*. This is, however, undoubtedly a mistake due to superficial resemblance. *Lachnocladium* is a typical member of the Thelephoraceae, characterised by having one side of the sporophore fertile, or covered with the hymenium, while the other side is sterile and protective. A section at once reveals the true structure. *Acurtis*, included by Saccardo under the Clavariaceae, is a spurious genus founded on abnormal growth.

In the Ascomycetes the genus *Xylaria* has the sporophore clavate, and either simple or branched, and superficially resembling species of *Clavaria*, from which it is distinguished by the absence of basidia, and the presence of asci.

Finally, some authors have removed the genus *Sparassis* from the present family and placed it in the Thelephoraceae. This is undoubtedly a mistake. As already stated, one surface of the sporophore is always sterile; in other words, the hymenium is confined to one surface in the last-named family, and the whole structure is tough and elastic. In *Sparassis* the substance is crisp and very brittle, and both surfaces of the folds of the sporophore are covered by the hymenium, as in all species included in the Clavarieae.

Thelephoreae

The dominant character of this family is the even surface of the hymenium. In *Hypochnus*, the most primitive genus, the characteristic feature of the Hymenomycetes, that is, a continuous, compact spore-bearing surface or hymenium, is absent, and it is only owing to the presence of typical basidia that it is included in the Basidiomycetes. The sporophore consists of very loosely interwoven hyphae trailing over the substratum, like some mould, and the tetrasporous basidia are produced in small, scattered clusters. *Hypochnus* is very closely allied to *Zygodesmus*, a genus usually placed in the Hyphomycetes or moulds, belonging to the heterogeneous collection of conidial forms included in the 'Fungi imperfecti.' *Zygodesmus* differs from *Hypochnus* in the less differentiated basidia bearing a variable number of sterigmata. Clamp-connections are very conspicuous on the hyphae. All the other genera included in the Thelephoraceae have a typical compact hymenium. In two genera, *Coniophora* and *Corticium*, the thin sporophore is resupinate or attached by its entire under sterile surface to the substratum. The hymenium in both genera is perfectly even, and there are no cystidia. There is also an absence of a subhymenial layer, that is, a compactly interwoven zone of hyphae situated between the lower vegetative hyphae of the sporophore and the hymenium. In all other genera included in the Basidiomycetes this subhymenial stratum is present, and gives origin to the basidia.

Next follow in order the genera *Peniophora* and *Hymenochaete*. The simplest types in both genera are entirely resupinate as in *Corticium*, but in the more advanced species the uppermost portion of the sporophore becomes free from the matrix, and projects at right angles to it, the hymenium being on the under surface of the free portion of the sporophore, and pointing to the ground. In both genera the hymenium is perfectly even, and densely crowded with cystidia. In *Peniophora* the cystidia are colourless, thin-walled, and eventually become rigid, due to a superficial crust of amorphous particles of lime. When young the cystidia appear to act as organs of transpiration; very minute drops of water containing the lime salt in solution are liberated by the cystidia, and as the water evaporates, the lime is deposited as a solid, superficial crust. By this means the cystidia are rendered very brittle, and are often broken away in old specimens, leaving the hymenium bald and smooth. In *Hymenochaete* the cystidia are brown in colour, thick-walled, and not at all incrusted with lime. Next in the sequence of evolution comes the genus *Stereum* ; the hymenium is still perfectly

FIG. 102.—*Corticium scutellare.* The sporophore is adnate, or closely adherent to the matrix at every point, and the upper, exposed surface is entirely covered by the hymenium. Nat. size.

even, and cystidia are absent. There is a distinctly marked subhymenial layer, which readily separates resupinate

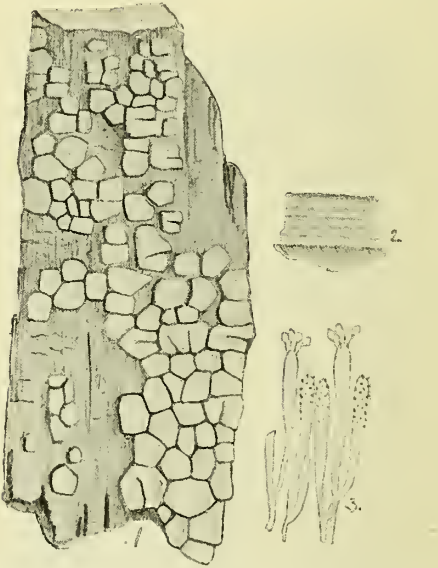

FIG. 103.—*Stereum frustulosum*, one of the simpler forms of *Stereum* having the sporophore entirely adnate to the matrix as in *Corticium*. 1, a dense group of plants growing on a piece of oak wood; 2, section through the sporophore showing several distinct zones or layers, a feature characteristic of this species; 3, section of a portion of the hymenium, showing two basidia, each bearing four spores at its apex, also three paraphyses roughened on the surface with minute particles of oxalate of lime. Fig, 1, nat. size; the others mag.

species of *Stereum* from *Corticium*. In the simplest forms the sporophore is adnate, in others laterally attached to the substratum, whereas in the most perfect species there is a truly central stem supporting a funnel-shaped pileus,

FIG. 104.—*Stereum hirsutum*, a fungus having a sporophore which is partly adnate to, or lying flat and attached to. the matrix, whereas the upper portion of the sporophore is free from the matrix, and grows at right angles to it. The hymenium or spore-bearing portion is on the under side of the free portion ; the upper side is sterile and protective. 1, fungus growing on a piece of dead wood; 2, section of same; 3, basidia, each bearing four spores. Figs. 1 and 2, nat. size; fig. 3, mag.

bearing the hymenium on its under surface. In many of the lateral-stemmed species of *Stereum* the pileus is often cut into narrow lobes, whereas in the allied genus *Lachnocladium*, which grows erect from a short, stem-like base, the branches are so narrow and so numerous that the species are superficially confounded with branched species of *Clavaria*. The mistake is corrected on examining a section which in *Lachnocladium* has the hymenium confined to one side of the sporophore, whereas in *Clavaria* the hymenium entirely surrounds the sporophore.

Although, as already stated, the even hymenial surface is the hall-mark of the Thelephoreae, as a matter of fact the genera remaining to be considered have the surface of the hymenium more or less uneven, and shadowing in, as it were, those features which become of primary importance when fully evolved in allied families.

Cladoderris, an exotic genus with a fan-shaped pileus attached laterally by a very short stem, has the hymenium rugulose and more or less covered with blunt projections, suggesting the more highly differentiated, blunt, tooth-like projections on the hymenium of *Radulum*, belonging to the Hydnaceae. On the other hand, *Craterellus*, belonging to the Thelephoreae, has a central stem and funnel-shaped pileus, and the inferior hymenium has more or less pronounced veins or wrinkles running from the margin of the pileus to the stem, and resembling very closely in habit and general structure the genus *Cantharellus*, belonging to the Basidiomycetes, where the gills more resemble thick, blunt-edged veins, than the thin, sharp-edged gills characteristic of the last named-order.

In the present family the spores vary from colourless, through pale yellow to deep ochraceous in different genera.

Representatives of the family are met with everywhere, being most abundant in temperate regions, yet the most highly evolved forms are tropical. Species of *Coniophora*, *Corticium*, *Stereum*, etc., form extended crusts on trunks, logs, posts, etc.

Two genera, *Cora* and *Rhipidonema*, at one time included in the present family, are now known to be lichens, and constitute the group known as Basidio-lichens, on account of the fungal element belonging to the Basidiomycetes. Both are tropical genera, having a semicircular or fan-shaped pileus attached laterally, and would have been species of *Stereum* but for the presence of an algal element in the pileus.

Hydneae

On this family the hymenium is borne on spine-like processes crowded together, taking the place of tubes in the Polyporaceae, and gills in the Agaricineae. In *Hydnum*, the central and most highly evolved genus in the family, the spines are densely crowded, and in some species from two to three centimetres in length. In the genus *Phlebia*, which forms a bridge from the Thelophoreae to the present family, the hymenial surface is simply rugulose, the edge of the wrinkles being vaguely corrugated or toothed; in *Irpex* the teeth or spines are more pronounced, but still originate from anastomosing folds or ridges. *Radulum*, with coarse, irregular, subcylindrical but obtuse teeth or spines, leads up to *Hydnum*. In *Odontia* the spines are reduced to mere projecting granules, having the tips fringed or minutely fimbriate. The conception of the hymenium being borne on spines, although affording a considerable amount of surface at the cost of a small amount of material, has not been extended beyond the Hydnaceae, which thus may be looked upon as a terminal group.

Several genera have the sporophore constantly resupinate or adnate throughout, and even in *Hydnum*, numerous of

FIG. 105.—*Hydnum scheidermayeri*. Entire fungus; very much reduced in size.

the simpler species are of this type, whereas some of the largest species, which sometimes exceed a football in size, are attached laterally, and consist of a compact fleshy mass, the front and lower surface bearing long, crowded, pendulous spines. The highest types of *Hydnum* have a central stem, and a veil is present in some species.

There is a marked absence of bright colours, the prevailing tints ranging from pallid through buff to brown or dusky.

Some few species are edible; none are known to be poisonous.

The spores are colourless or very slightly tinted, and altogether there is an absence of breaks in new directions as compared with other families. Cystidia are not known to be present.

The simple, resupinate species grow on dead wood; some of the large dimidiate forms are parasitic on trees; the central-stemmed species grow on the ground. The home of the family is in the north temperate and subarctic zones; in fact, so far as is known of their distribution at the present time, it may be said that a greater number of the higher types of *Hydnum* grow in the forests of Sweden than in all the other parts of the world put together. A few species are known from the tropics.

Agaricineae

In the present family the common bond of union is the presence of thin flat plates of tissue called gills or lamellae, over which the hymenium is spread. These gills, in the case of central-stemmed species, radiate from the stem to the margin of the pileus, and in laterally attached forms radiate from the point of attachment of the fungus to its matrix. Shorter secondary and tertiary series of gills are interposed between the primary ones, that reach from the stem to the margin of the pileus, as the latter become more and more divergent. In all the higher forms the

FIG. 106.—*Lentinus cyathus*, an agaric springing from a sclerotium; the latter shown in section. The gills are deeply decurrent. One-sixth nat. size.

hymenium is inferior, or placed on the under surface of the pileus, and pointing to the earth. A lamella has three distinctly marked structural zones or layers. A central portion, called the trama, consists of more or less parallel hyphae continuous with the hyphae of the pileus. The trama is bounded on either side by a densely interwoven layer, the subhymenial layer, the hyphae of which give origin to the basidia and paraphyses, whose free tips form the surface of the lamella or gill. Cystidia originate from the hyphae of the trama, and not from those forming the subhymenial layer. In the genus *Schizophyllum* the free margin of the gill is split along the line of the trama for a very short distance inwards, the split halves respectively curling outwards or away from the split. A much slighter groove runs along the edge of the gill in the genus *Trogia*. In other genera the edge of the gill is entire and thin. In many species the gills are connected by ridges which spring from the substance of the pileus, but such connecting ridges are much shallower than the depths of the gills themselves.

In one genus, *Montagnites*, the pileus or upper sterile protective portion of the sporophore is entirely absent, the gills originate from the apical portion of the stem, and radiate like ordinary gills, but without any supporting membrane above. This genus is a native of the Egyptian desert, and the entire sporophore is at first enclosed in a volva buried in the sand; in this position the whole of its development takes place, and when the spores are ripe the volva is ruptured and the sporophore raised into the air on a tall stem. In all other genera the gills are attached throughout their length to the under surface of the pileus from which they originate. On the other hand, the relative amount of attachment, or entire freedom of the gills from the stem, is a matter of importance from a

FIG. 107.—*Armillaria mellea*, showing the sporophore or reproductive portion of the fungus, which consists of pileus or cap, bearing the gills which produce the spores, on its lower surface; stem; and secondary veil, a membrane which extends from the stem to the margin of the pileus, thus protecting the gills when young; at a later stage this membrane splits and breaks away from the pileus, shrinks and forms a ring or collar round the stem. The vegetative portion of the fungus is buried in the ground. Half nat. size.

systematic standpoint, and constitutes a most important generic character.

In the simpler types the gills run down the stem for some considerable distance, when they are described as decurrent; when the gills are attached to the stem by their entire width, they are said to be adnate; when cut out or rounded behind, so that only a portion of the width of the gill is attached to the stem, the term adnexed is used; whereas, when the gills are rounded off behind, so that they terminate before reaching the stem, they are said to be free; meaning free from the stem.

In the primitive types of the Agaricineae, illustrated by species belonging to the genera *Cantharellus*, *Pleurotus*, *Trogia*, etc., the sporophore is resupinate, that is, the imperfectly evolved pileus is in contact with the matrix, and the gills or hymenium uppermost. In such species the gills are rudimentary in structure, and often more resemble wrinkles or folds than gills as understood in the higher forms, and agree closely with the rugulose appearance of the hymenium in such genera as *Craterellus*, belonging to the Thelephorineae, the family from which the Agaricineae descended. A further stage of advance is seen in *Lenzites*, where the sporophore is attached to the matrix by a broad base, and the hymenium has become inferior. Following this is the dimidiate, flabellate, or semicircular pileus supported by a lateral stem, that is, a stem springing from the margin of the pileus. This type leads by degrees to the highest phase of sporophore development attained to by the Agaricineae, a pileus bearing the hymenium on its lower surface, and supported by a central stem. Even in this highest stage of development there are marked differences of degree. In the simplest stage

FIG. 108.—*Pholiota adiposa*, a typical Basidiomycete. 1, a cluster of sporophores, *a*, pileus, *b*, stem ; 2, section of pileus, *a*, *a*, lamellae or gills, *b*, *b*, the secondary veil ; 3, spores, technically conidia, as they are of a sexual origin. Figs. 1 and 2, half nat. size; fig. 3, highly mag.

the pileus, when young, is globose, with its margin incurved or pressed straight to the stem, and on expanding, the gills are at once exposed, and remain so until they are completely developed and the spores are mature. An advance on this arrangement is seen in those species provided with a secondary veil, which originates from the upper portion of the stem as a thin membrane, and is attached to the margin of the pileus. This membrane grows and keeps pace with the expanding pileus, thus concealing the gills until the spores are nearly mature, when it breaks away from the margin of the pileus and forms a collar or ring round the stem, or in some instances almost entirely disappears. In the highest type the entire sporophore is enclosed in a universal veil which is buried in the ground. After the pileus and gills are differentiated the universal veil is ruptured, and the sporophore is elevated above ground on a quickly growing stem, the universal veil remaining as a basal sheath round the stem, and now called a volva, or in many instances the upper portion of the universal veil adheres to the pileus, where it is torn into patches as the pileus increases in size. Some species furnished with a universal veil have also a secondary veil, thus protecting the hymenium until maturity; in other species the secondary veil is absent.

The primary divisions or sections of the Agaricineae are founded on the colour of the spores, an arrangement which is by no means artificial as it appears to be at first sight. The colour of the spores when thrown down in a mass on paper, and not as seen by transmitted light, is used for discriminating the sections, which are as follows:—Melanosporae, spores black. Porphyrosporae, spores purple-black. Ochrosporae, spores ochraceous brown or rust-colour.

Rhodosporae, spores salmon-colour or pinkish. Leucosporae, spores colourless or tinged yellow. Chlorosporae, spores pale dull green.

These sections have evolved in a definite sequence from each other, and each group commences with the most primitive resupinate forms, and passes through the sequence of structure indicated above, until the central-stemmed type is reached. Many of the larger genera show signs of repeating this spore differentiation, and the formation of new genera of groups, as *Naucoria* in the Ochrosporae, and *Russula* and *Lepiota* in the Leucosporae.

I have elsewhere, when dealing with *Coprinus*, shown that this genus, characterised by the gills becoming deliquescent at maturity, is probably the most primitive type of the Agaricaceae, and the starting-point of the sub-family Melanosporae, from which the other sub-families have evolved in the sequence given above.

Many species included in *Coprinus*, as *C. plicatilis* and others, having dry, non-deliquescent gills, have no real affinity with this genus.

In addition to the evidence afforded by morphology as to the order of appearance of the various sub-families, physiological factors are also in evidence. In the Melanosporae there is a total absence of those special by-products of metabolism under the form of poisons, which serve as protective agents; so far as is known, all members of the Melanosporae are edible, or at all events non-poisonous, whereas such substances begin to appear in the other sub-families, and when the Leucosporae are reached, poisonous products are very widely dispersed. A similar sequence is observable in the families of the Hymenomycetes. In the most primitive family, Clavariaceae, poisons are absent, whereas towards the other pole or most modern end, poisonous properties are very abundant.

The species are annual, those in temperate zones are mostly short-lived and putrescent, whereas the majority of forms occurring in the tropics are dry, corky, and tough, leading up to such genera as *Lenzites*, *Panus*, etc., which form a transition to the Polyporaceae.

Many species are edible, and a yet greater number are poisonous. Edible and poisonous species often occur as closely allied forms belonging to the same genus.

Polyporeae

The leading idea of the present family consists in the hymenium being composed of a series of closely packed tubes standing side by side, their free, open ends collectively forming the surface of the hymenium. The entire inner surface of each tube is covered with basidia and other elements of the hymenium, the spores falling out of the tubes into the air at maturity. In *Polyporus*, the central and most typical genus included in the family, the tubes, as seen in a section, are sometimes one to two centimetres in length, the diameter varying from a quarter to one millimetre.

As would be expected, all genera are not equally typical, those shadowing in the family from its predecessor, the Basidiomycetes, naturally retaining some of the structural features of that family. Among such may be noted the genera *Daedalea* and *Trametes*, where the hymenium is borne on irregular plates or gills radiating from the stem to the circumference of the pileus; but these gills are variously connected by transverse walls, which are sometimes placed so close together as to resemble irregular pores. In both the genera named it is not unusual to find one portion of the hymenium of a specimen distinctly

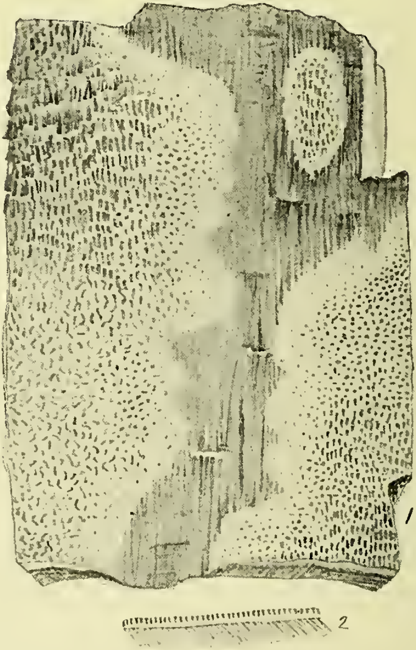

FIG. 109.—*Poria vaporaria*, showing the adnate sporophore covered on the free surface with irregular pores. This is one of the commonest of British fungi, growing on dead fallen branches, etc. Nearly nat. size.

lamellar or gill-like in structure, whereas another portion is as distinctly composed of pores or tubes. In some species of *Merulius* the tubes are exceedingly shallow and of irregular shape and size, being formed by the anastomosing of slightly raised ribs or veins. In *Hexagonia*, a beautiful tropical genus, the pits or tubes forming the hymenium are regular polygons, not always hexagons, as implied by the generic name, and in some species they are of large size, presenting the appearance of honeycomb, hence the name of one species, *Hexagonia apiaria*. It

FIG. 110.—*Polyporus hispidus*, parasitic on various trees. 1, two sporophores seen from the front; 2, section showing fleshy pileus, *a*, and long tubes, *b*; 3, two basidia with spores. Much reduced.

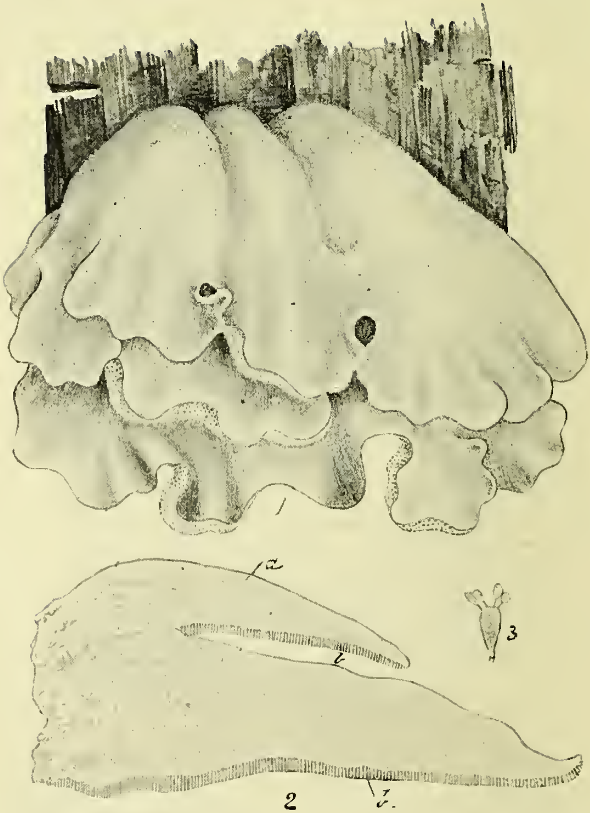

FIG. 111.—*Polyporus sulphureus*, a parasite on various trees. 1, a group of sporophores seen from above; 2, section showing very fleshy pileus with very short tubes on the under surface, *a*, pileus, *b*, *b*, pores; 3, basidium bearing four spores. Much reduced.

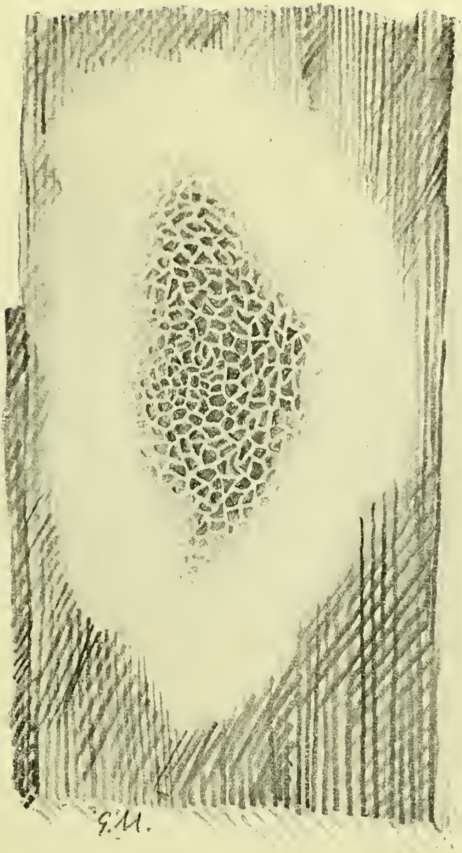

FIG. 112.—*Merulius lacrymans*, 'dry rot,' showing the adnate sporophore with a broad white, floccose, sterile margin; in the central portion the hymenium composed of shallow, irregularly shaped pores. Reduced.

is interesting to note that in the present family, the most highly evolved of the Basidiomycetes, there is represented every phase in the evolution of the families preceding it. In the structure of the sporophores we meet with a thin crust adnate throughout to the matrix in species of *Merulius*. Sporophores attached laterally by a broad base to the matrix, with the hymenium on the under side, and resembling an inverted bracket or a horse's hoof, are numerous in the genera *Polyporus*, *Trametes*, etc. A more advanced phase of development is illustrated by *Polyporus squamosus*, common in Britain and elsewhere, growing from some injured portion of the trunk of a tree; here we have a large, flat, fan-shaped or semicircular sporophore with a short, almost lateral stem. Perfectly

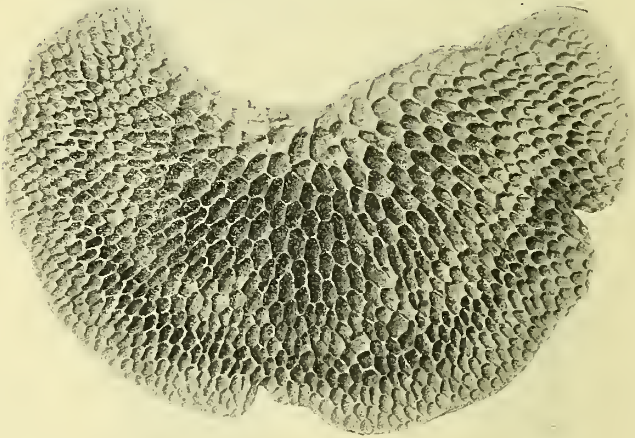

FIG. 113.—*Hexagonia apiaria*, showing very large polygonal pores. The genus *Hexagonia* is mostly confined to tropical and subtropical regions.

central-stemmed species of *Polyporus* are not uncommon in tropical countries, but are rare in Europe. A few species of *Polyporus* spring from sclerotia; in one Australian form, *Polyporus mylittae*, the sclerotium is sometimes as large as a child's head, and is as hard and dense as the hardest wood when dry. Central-stemmed forms of this family are best represented in the northern hemisphere by the genus *Boletus*. The species are usually large, grow on

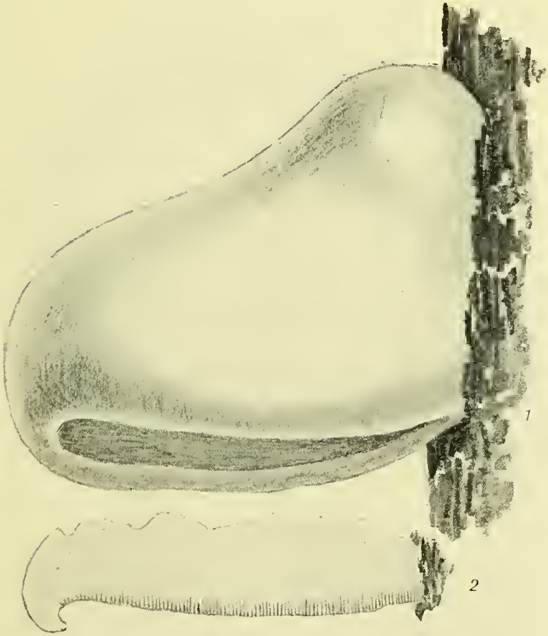

FIG. 114.—*Polyporus betulinus*, a parasite on birches. 1, sporophore with incurved margin, and showing the hymenium on its lower surface; 2, section of thick, fleshy sporophore with incurved margin, and very short tubes on its under surface. Reduced.

the ground, and superficially resemble a large toadstool from above, but instead of gills, the under surface consists of closely packed tubes with the open ends pointing downwards. The entire mass of tubes separates quite readily

FIG. 115.—*Fomes fomentarius*, a large perennial fungus having a hard, woody sporophore. The upper surface is sterile, the hymenium being situated on the flattened under surface. A new hymenial layer is formed each season upon the previously existing one. The different layers of hymenial tissue are indicated by lines as shown in the section. Each layer extends a little beyond the previous one, hence the hymenium increases in area each year. The ridges on the surface roughly correspond to the number of hymenial layers. One-quarter nat. size.

from the flesh of the pileus. Some species of *Boletus* have a well-defined collar on the stem, which is attached to the margin of the pileus during the young stage. A similar structure is indicated in some kinds of *Polyporus*.

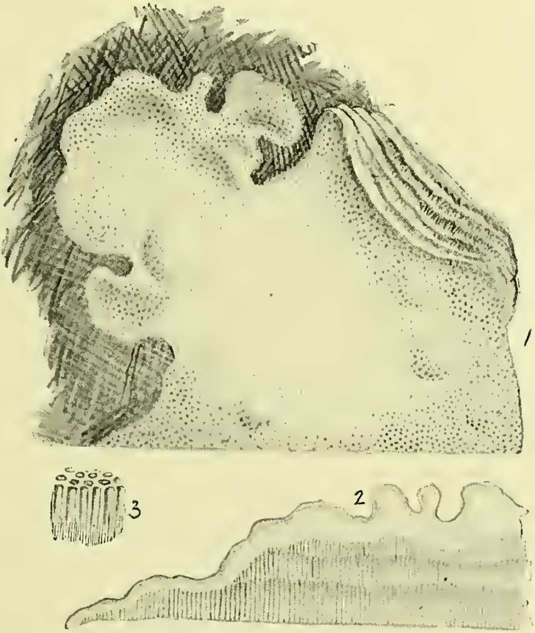

FIG. 116.—*Fomes annosus*, a parasite on various conifers, attacking the root. 1, a portion of a sporophore; 2, section of sporophore showing three strata of tubes; 3, showing the mouths or pores of the tubes. Figs. 1 and 2, nat. size; fig. 3, slightly mag.

Many of the giants of the fungal world are members of the present family. *Fistulina hepatica*, the beefsteak fungus, sometimes attains to a large size, and has been recorded as weighing thirty pounds. Many species of *Polyporus* often reach or sometimes exceed a foot in diameter, and when perennial become very hard and woody.

Some species of *Polyporus* are destructive wound-parasites, attacking trees.

Among edible kinds may be enumerated several species of *Boletus*, more especially *B. edulis*, also *Fistulina hepatica*. Many species of *Boletus* are poisonous.

In the majority the spores are minute, but in *Boletus* they are exceptionally large, more or less spindle-shaped and coloured. In *Strobilomyces*, a genus superficially resembling *Boletus*, the spores are globose, warted, and coloured.

Cystidia are present in abundance in some species of *Polyporus*.

The distribution of the family is cosmopolitan. The majority grow on wood.

Conidial forms have been described as present in cavities in the young pileus of *Fistulina hepatica* by De Seynes. The conidial forms of some species of *Polyporus* are produced on a body of considerable size preceding the formation of the sporophore. This conidial condition was at one time accepted as a distinct genus of fungi called *Ptychogaster*.

GASTEROMYCETES

The subterranean forms included in the Hymenogastraceae are almost universally considered as the most primitive types, and starting-point of the present group; but apart from the indehiscent nature of the protective portion of the sporophore, called here a peridium, there are no indications of morphological inferiority as compared with other families. Usually the entire structure enclosed within the peridium consists of plates of tissue whose free surfaces are covered with the hymenium; the entire mass is here called the gleba. The plates forming the gleba have precisely the same structure as the gills in Agaricineae. There is a central trama bounded on either side by a denser subhymenial layer, from which the elements of the hymenium—basidia and paraphyses—originate. These plates anastomose at numerous points, the result being a sponge-like or cavernous structure, the walls of the cavities bearing the hymenium. The plates in all families except the Phalloideae are attached on all sides to the inner surface of the peridium. In some families a large number of long, tapering, simple, or branched hyphae, collectively constituting the capillitium, and having to do with the dispersion of the spores, are present in the gleba. These capillitium threads originate from the hyphae of the trama, and may be considered as homologous with cystidia, so frequently met with in the Basidiomycetes.

In the Lycoperdaceae, at a certain stage of development, after the formation of the spores, the entire mass of the gleba presents a water-logged appearance. This is due to the deliquescence of the elements of the hymenium—basidia and paraphyses—and the tramal plates, the spores and capillitium threads alone remaining. Eventually these become dry, and form a pulverulent mass, consisting of spores and capillitium threads. In the Nidulariaceae, or 'bird's nest' fungi, the tramal walls split and become hardened and permanent, enclosing the spores that were borne on the wall of the cavity. There are thus as many of these sealed-up portions, called peridiola, as there were originally cavities in the gleba. Conidia are unknown.

KEY TO THE FAMILIES

A. **Subterranean**

Sporophore fleshy, indehiscent, subglobose, or irregularly nodulose; gleba cavernose, not breaking up and becoming pulverulent. Capillitium absent. *Hymenogastereae.*

B. **Sporophore above ground from the first, or at maturity**

Peridium thick, not differentiated into layers, rupturing irregularly; gleba cavernose. Spores not forming a powdery mass; capillitium absent. *Sclerodermeae.*

Peridium of one or two layers, containing several (rarely one) lenticular or subglobose sporangiola; spores not forming a pulverulent mass; capillitium absent. *Nidularieae.*

Peridium thin, consisting usually of two layers, dehiscent as a rule; gleba at first cavernous, breaking up into a powdery mass of spores mixed with hyphae forming a capillitium. *Lycoperdeae.*

Volva with a middle gelatinous stratum; spores embedded in mucilage at maturity. Capillitium absent. *Phalloideae.*

Hymenogastereae

This family agrees with Tuberaceae in its subterranean habit, also the superficial appearance, but differs in producing its spores on basidia. Most of the species are irregularly globose, and in many cases originate from a dense weft of mycelium. A further coincidence is the strong smell emanating from some species in both families. The basidia are very variable in form, and in the number of spores they bear. The spores are often large, dark coloured, and have surface markings, warts, network, etc. The peridium is indehiscent, and its wall not differentiated into layers.

Most species grow under trees, and several have only been met with in the proximity of certain kinds of trees, suggesting parasitism or the formation of mycorrhiza, as is known to exist between species of *Elaphomyces* and fir-trees.

So far as at present known, most abundant in Europe, but their subterranean habitat is against their discovery by the traveller in other countries.

Sclerodermeae

Peridium thick, wall not differentiated into layers, dehiscing by a gradual disintegration at the apex, or by splitting into irregular valves. The spores are small, yet there is no definite arrangement for their dispersion as in the Lycoperdaceae. In *Scleroderma* the tramal plates disappear, but the gleba does not become pulverulent. In *Polysaccum* the tramal plates are permanent, and form sporangiola.

Distinguished from Hymenogastereae by the well-defined sterile base of the peridium, which sometimes becomes elongated as a stem.

Distribution general.

Nidularieae

Small fungi, not having the peridium wall splitting into separate layers, although layers are differentiated in *Cyathus*. The walls of the trama become indurated, and the resulting peridiola eventually lie loose in the cavity of the peridium, which opens at the apex. To this appearance is due the popular name of bird's-nest fungi, the open peridium resembling the nest, and its contained sporangiola the eggs. In *Sphaerobolus* the single sporangiolum is elastically ejected to a considerable distance when mature.

Generally distributed.

Lycoperdeae

This family includes the puff-balls—*Lycoperdon*, and earth stars—*Geaster*.

The peridium wall is differentiated into two distinct layers, which separate from each other. In *Bovista* the outer layer of the wall breaks away in flakes. In *Lycoperdon* the outer wall of the peridium is differentiated into spines or mealy warts that disappear as the fungus reaches maturity. This outer layer is the exoperidium; the inner persistent layer enclosing the spores, the endoperidium. In *Geaster* the exoperidium splits from the apex into a variable number of pointed lobes which spread out like rays, hence the popular name, earth-star. The endoperidium is filled at maturity with a powdery mass of spores mixed with elastic capillitium threads, which escape through a perforation at the apex of the peridium. In the genus *Myriostoma* several perforations for the escape of the spores are scattered over the surface of the peridium, which resembles the lid of a pepper-pot. *Podaxon* is a genus met with in South Africa, where it is said to be common on deserted ant-hills. The general aspect of the fungus is that of *Coprinus comatus*. The stem is six to nine inches long, and passes quite through the gleba, and is attached to the apex of the peridium. The latter, when the spores are mature, breaks away at its base and expands, allowing the spores, as it were, to fall out. The fact that this species is common on deserted ant-hills suggests the idea that when the ants are in residence, they utilise this fungus for the formation of a fungus-garden, and feed on a conidial form, as is practised by ants and termites in other countries, and with other kinds of fungi.

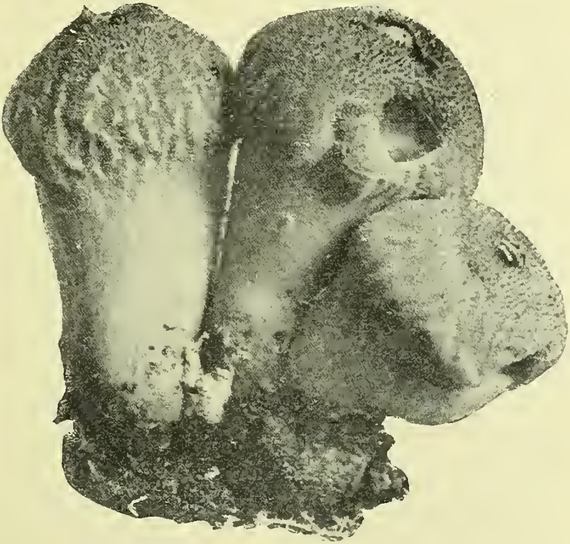

FIG. 117.—*Lycoperdon gemmatum*. Nat. size. (After Lloyd.)

Widely distributed in all countries.

Phalloideae

This family is characterised by having the central layer of the peridium gelatinous at maturity. Another feature consists in the spores, which are exceedingly minute, being embedded in a greenish, fetid slime derived from the deliquescent elements of the hymenium.

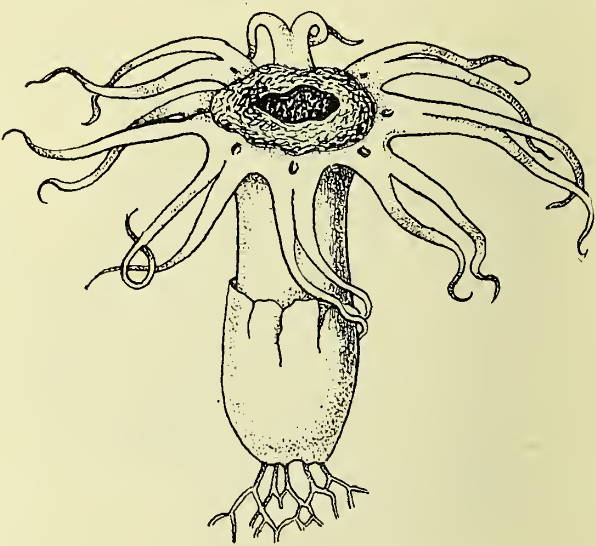

FIG. 118.—*Aseröe rubra*, an insect attracting fungus belonging to the Phalloidaceae. The stem and the sheathing volva at the base, which originally enclosed the whole plant, are white. The spreading rays, which are attractive on account of their brilliant crimson colour, also serve as a landing-stage for insects, from which they can devour the dark, central, slimy, sweet substance containing the spores. Two-thirds nat. size.

FIG. 119.—*Phallus impudicus*, a fungus very common in English woods. The smell is very strong and unpleasant. The upper rugged thimble-like portion bears the hymenium. The torn sheath at the base of the stem is the volva, in which the whole plant was enclosed when young and underground. About half nat. size.

When in a young condition the hymenium, as usual, is enclosed in a whitish, soft peridium, and the first period of growth takes place underground. When the spores are formed the hymenial portion of the fungus ruptures the peridium, and becomes elevated into the air on a long stem. The ruptured peridium, with its thick, gelatinous, middle layer, remains as a sheath round the base of the stem, and is then called a volva. The sporophore assumes some very quaint forms in the various genera. In *Phallus* it resembles a thimble poised on the top of a long stem. In *Clăthrus* it takes the form of a hollow sphere formed of irregular lattice-work, whereas in *Aseröe* it consists of several spreading rays resembling a starfish.

FIG. 120.—Hymenium of *Phallus impudicus* partly covered with olive-green mucus, in which the very minute spores are embedded. Several flies are present devouring the mucus. Nat. size.

The sporophore is usually red, smeared more or less with the green, fetid slime containing the spores. This slime is greedily devoured by flies, its whereabouts being indicated by the penetrating smell, aided by the bright red colour; by this means the spores are disseminated.

The species are most abundant in tropical countries; there are about half-a-dozen outlying species in Europe, three of which are British. Our commonest form, *Phallus impudicus*, has a whitish sporophore, whereas the same structure is red in *Mutinus caninus*, and bright red in the beautiful but abominably fetid *Clathrus cancellatus*.

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DEUTEROMYCETES

The members of the present group of fungi have of late years been considered to represent conidial forms of the Ascomycetes and Basidiomycetes, and by philosophical mycologists are usually very briefly alluded to under the designation of 'Fungi imperfecti.' This line of reasoning is supported by the fact that several forms have been absolutely proved to be only phases in the life-cycle of higher species. As examples may be mentioned such form-genera as *Uredo*, *Aecidium*, *Tubercularia*, *Oidium*, *Botrytis*, *Isaria*, etc.

There remain, however, some thousands of forms that as yet have not been connected with any of the higher species, and, as previously stated, it is the business of the systematist to carefully describe and tabulate such so that they can be recognised.

Tulasne was the first to clearly indicate that various forms of fruit were produced by the same fungus at different periods of its development; this discovery was the outcome of observing the constant sequence of forms originating from the same mycelium or stroma. The method of growing one phase of a fungus from the spores produced by another phase has in some instances corroborated Tulasne's observations.

From an economic aspect the Deuteromycetes are of primary importance, as nearly all plant and animal diseases caused by fungi are primarily due to infection by the conidial form of fruit.

There is a total absence of sexuality in the present order, and all the varied forms of reproductive bodies produced are truly conidia, although in systematic works spores and conidia are often used indiscriminately.

The forms are almost invariably minute, although owing to the gregarious habit of many kinds, large and conspicuous patches are produced which are often brightly coloured.

The order is divided into three sub-orders, Sphaeropsidiaceae, Melanconiaceae, and Hyphomycetaceae. In the Sphaeropsidiaceae the fruit is angiocarpous; that is, the conidia are produced in a definite perithecium as in the Sphaerieae, but there are no asci, the conidia being produced at the tips of simple or branched conidiophores, which originate from the inner cells forming the wall of the perithecium. The conidia are often involved in mucus, and escape from the ostiolum or opening of the perithecium in long, tendril-like masses.

In the Melanconiaceae the fruit is hemiangiocarpous, or partly surrounded by a more or less saucer-shaped perithecium or excipulum, from the inner surface of which the conidiophores spring in large numbers. This arrangement is analogous to the arrangement of the asci in the more or less open cup-shaped structure met with in the Discomycetes. It is, however, important to bear in mind that no affinity or relationship is indicated by this agreement in structure.

In the Hyphomycetes the fruit is strictly gymnocarpous, that is, there is no trace of any perithecium or outer sterile protective covering present. The conidiophores spring directly from the vegetative hyphae under the form of simple or variously branched, usually upright threads, and bear the conidia either solitary or in chains at the tips of the branchlets.

KEY TO THE SUB-ORDERS

Perithecium present, asci absent, conidia produced on minute conidiosphores springing from the inner cells of the perithecium. *Sphaeropsidiaceae.*

Perithecia and asci absent, fruiting cushion soft, erumpent from an immersed, stroma-like base; conidia borne on closely crowded conidiophores. *Melanconiaceae.*

Perithecia, asci, and immersed stroma absent; superficial or almost so, conidiophores erect, often branched and bearing the naked conidia at the tips of branchlets. *Hyphomycetaceae.*

SPHAEROPSIDIACEAE

In the present order the conidia are produced within a highly differentiated perithecium, resembling in many essentials that present in Sphaeriaceae; asci, however, are absent, the conidia being borne on the tips of slender hyphae springing from the inner cells of the perithecium.

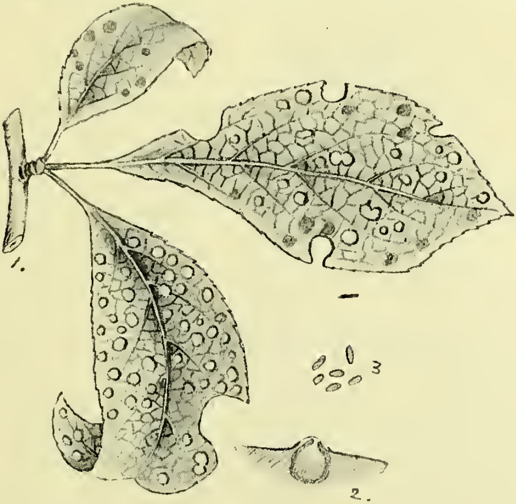


FIG. 121.—*Phyllosticta prunicola*, a parasite on the leaves of various rosaceous fruit-trees. 1, apple leaves showing holes formed by the falling away of local patches killed by the fungus; 2, section of a perithecium embedded in the tissue of the leaf; 3, conidia produced in the perithecium. Fig. 1, slightly reduced; the others mag.

KEY TO THE FAMILIES

Perithecia membranaceous, carbonaceous, or subcoriaceous, black (never soft and fleshy, and bright or clear

in colour), globose or somewhat depressed, immersed or superficial; mouth or ostiolum circular, never elongated.
Sphaeroideae.

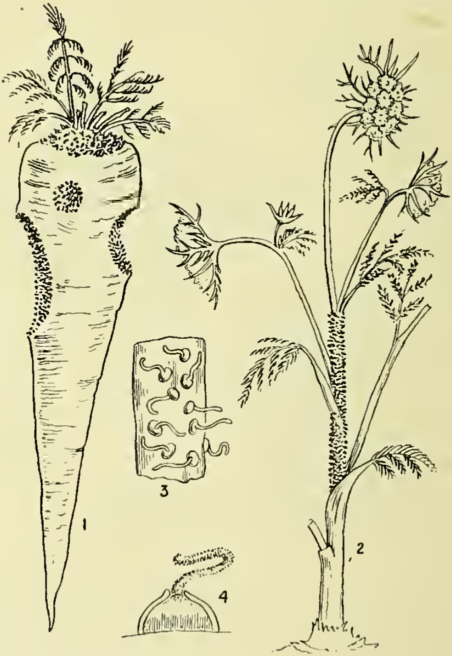


FIG. 122.—*Phoma sanguinolenta*, a parasite on cultivated carrots, etc. 1, a diseased carrot root; the fungus forms deep wounds in the substance of the root, on the surface of which the perithecia are densely aggregated; 2, diseased stem of carrot; 3, portion of a diseased spot showing perithecia emitting masses of conidia in mucilaginous, tendril-like strings; 4, section of a perithecium with a tendril of spores. Figs. 1 and 2, reduced; remainder mag.

Perithecia and stroma, when present, rather soft and fleshy, never carbonaceous, bright or clear in colour (whitish, yellow, orange or reddish), never dusky; subglobose, rarely elongated or somewhat concave; conidia various in form, hyaline. *Nectrioideae.*

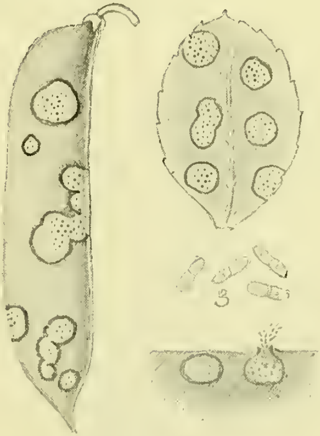


FIG. 123.—*Ascochyta pisi*, figs. 1 and 2, pod and leaflet of garden pea respectively attacked by the fungus, which forms bleached dead patches bounded by a dark line; 3, section of two conceptacles embedded in the substance of the host: the conidia shown above are more highly mag. Figs. 1 and 2, nearly nat. size; the remainder mag.

Perithecia more or less distinctly dimidiate, scutelliform or shield-like, mouthless or dehiscing by more or less elongated cracks or fissures, membranaceous or carbonaceous, black, erumpent or superficial. *Leptostromeae.*

Perithecia depressed, plane or circular, or elongated, sometimes subglobose at first, but soon becoming widely open or saucer-shaped, membranaceous or carbonaceous, black; erumpent or superficial, glabrous or hairy. *Excipuleae.*

Sphaeroideae

All the species are individually very minute, but owing to their gregarious habit often form conspicuous, broadly extended patches. In *Phyllosticta*, a genus containing between three and four hundred species for the most part parasitic on living leaves, the perithecia are densely gregarious on bleached spots; the perithecia are immersed in the substance of the leaf and covered by the epidermis, through which the ostiolum or mouth protrudes. The genus *Phoma*, containing several hundred forms, is saprophytic in habit, the minute, flask-shaped perithecia being usually grouped in dense clusters, and forming, to the naked eye, greyish or blackish stains on dead leaves, herbaceous stems,

FIG. 124.—*Entomosporium maculatum*. 1, quince leaf showing blotches formed by the fungus; 2, conidia with four slender appendages. Fig. 1, nearly nat. size; fig. 2, mag.

etc. The conidia are very minute and colourless, and often emerge from the mouth of the perithecium under the form of threads or tendrils, consisting of myriads of conidia held together by mucus.

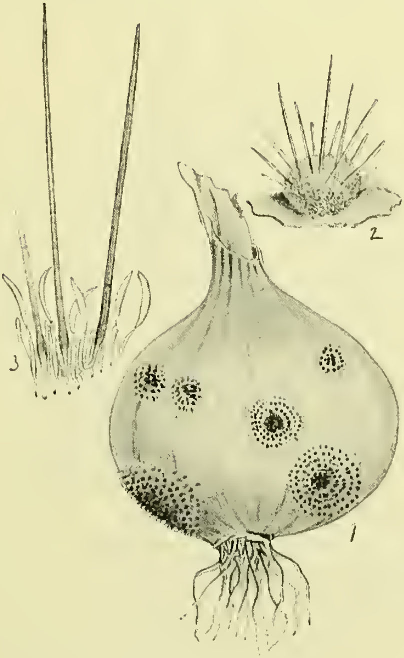


FIG. 125.—*Vermicularia circinans.* 1, an onion attacked by the fungus: the minute black fruiting bodies are arranged in concentric circles; 2, one of the fruiting bodies of the fungus, showing the sterile black spines springing from the sporodochium or conidia-bearing body; 3, section through a sporodochium, showing the short, simple conidiophores bearing the narrow, curved conidia: two black sterile spines are also present. Fig. 1, nat. size; the remainder mag.

Many genera are considered to be conidial conditions of Sphaeriaceous fungi; but in the great majority of instances the only evidence forthcoming is the constant sequence of development of such conidial and ascigerous forms.

FIG. 126.—*Gloeosporium nervisequum*, a destructive parasite on leaves of various species of *Platanus*. 1, leaf of a plane-tree attacked by the fungus, which follows the principal veins of the leaf; 2, conidia. Fig. 1, reduced; fig. 2, mag.

Nectrioideae

A small family of minute forms, mostly saprophytic on dead wood, bark, etc. The species are of a soft, somewhat fleshy consistency, and usually brightly or clearly coloured, superficially in these respects resembling the ascigerous family Nectrieae. *Zythia*, the largest genus, is suspected as representing a conidial form of the genus *Nectria.*

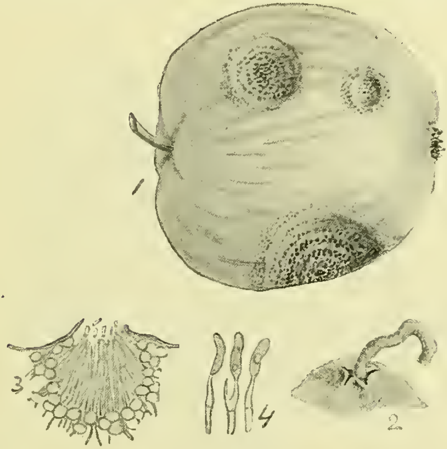


FIG. 127.—*Gloeosporium fructigenum*, a parasite on apples and other fruit. 1, appearance of the disease on an apple: the diseased patches become depressed owing to the destruction and collapse of the cells, and soon become studded with the pustules of fruit arranged more or less in concentric circles; 2, apex of one of the fruit pustules emitting a mucilaginous tendril of minute conidia through a crack in the epidermis of the apple; 3, section through one of the fruit pustules, showing the slender conidiophores bearing conidia at their tips; 4, three conidiophores, each bearing a conidium. Fig. 1, reduced; the others mag.

Leptostromeae

A small family consisting of very minute forms growing on dead or dying leaves, twigs, etc. In most species the

FIG. 128.—*Gloeosporium ampelophagum*, a destructive parasite attacking the vine. 1, appearance of the disease on a leaf, stem, and tendril of the vine; 2, diseased patches on grapes; 3, section through a pustule of fungus fruit produced on a young grape; 4, conidia. Figs. 1 and 2, reduced; the others mag.

perithecium is more or less flattened or shield-like, blackish in colour.

Excipuleae

A small family characterised by the minute, blackish perithecia becoming more or less depressed or saucer-shaped when mature. The wall and margin of the perithecium is often pilose.

MELANCONIACEAE

The perithecium is entirely absent in the present group ; there is usually a compact mass of hyphae located in the substance of the substratum, and from this the fruiting surface, consisting of a densely crowded mass of conidiophores, originates, and becomes erumpent, or bursts through the matrix to liberate the conidia in the air. The fruit masses are usually dusky or greyish, less frequently brightly coloured.

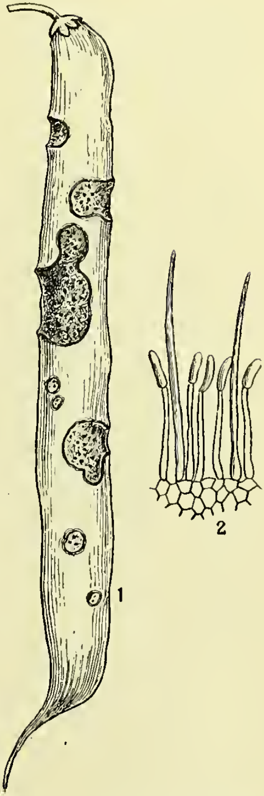


FIG. 129.—*Colletotrichum lindemuthianum*, a parasite attacking the pods of French beans, scarlet runners, etc. 1, a diseased pod of a scarlet runner: the fungus causes large, irregularly shaped patches of dead tissue, bounded by a dark line; 2, section through a fruit pustule showing elongated conidiophores, each bearing a conidium at its apex; two elongated, sterile, spine-like hyphae are also shown. The genus *Colletotrichum* only differs from *Gloeosporium* in having long, sterile spines mixed with the conidiophores. Fig. 1, slightly reduced; 2, mag.

Many species are destructive parasites, more especially those included in the genera *Gloeosporium*, *Colletotrichum*, *Pestalozzia*, and *Melanconium*.

FIG. 130.—*Pestalozzia guepini*, a parasite on leaves of the tea plant, *Camellia*, etc. 1, blotches formed by the fungus on a tea leaf; 2, conidia of the fungus: these are produced on simple or branched conidiophores, and have three or four very delicate hyaline cilia at the apex. Fig. 1, slightly reduced; fig. 2, highly mag.

HYPHOMYCETES

Saprophytes or parasites, superficial or nearly so on the matrix, sometimes internal parasites in the bodies of insects and other animals; hyphae transversely septate, usually copious; conidiophores bearing naked conidia (angiocarpous).

The species are mostly minute, and come under the designation of microscopic fungi, and are popularly known as ‘moulds,’ although this term is somewhat vague, and is also used for certain members of the Phycomycetes, as *Mucor*, etc.

Most species are gregarious, and form white or coloured, cottony or velvety patches, on decaying or dead plants, insects, etc.; some species, however, are destructive parasites. In some species the conidia are borne singly at the tips of hyphae, in others clusters of conidia are produced, and in a few species the heads of conidia are involved in mucus, and thus superficially resemble the heads of *Mucor*, where the conidia are contained within a cell or sporangium.

When mature the conidia fall away from the conidiophore very readily, and are distributed by wind, insects, birds, etc. If placed in water for examination the conidia separate from the conidiophore at once, so that their mode of attachment cannot be observed, but if placed in glacial acetic acid they remain attached, and can then be stained and mounted in balsam or other media.

KEY TO THE FAMILIES

Hyphae pallid or brightly coloured, flaccid or collapsing, and not cohering to form a compound, stem-like structure; conidia hyaline or clear coloured. *Mucedineae.*

Hyphae dark coloured, brown, olive, or blackish, rather rigid, often crowded, but not fasciculate, rarely almost hyaline, but in that case the conidia are dark coloured. *Dematieae.*

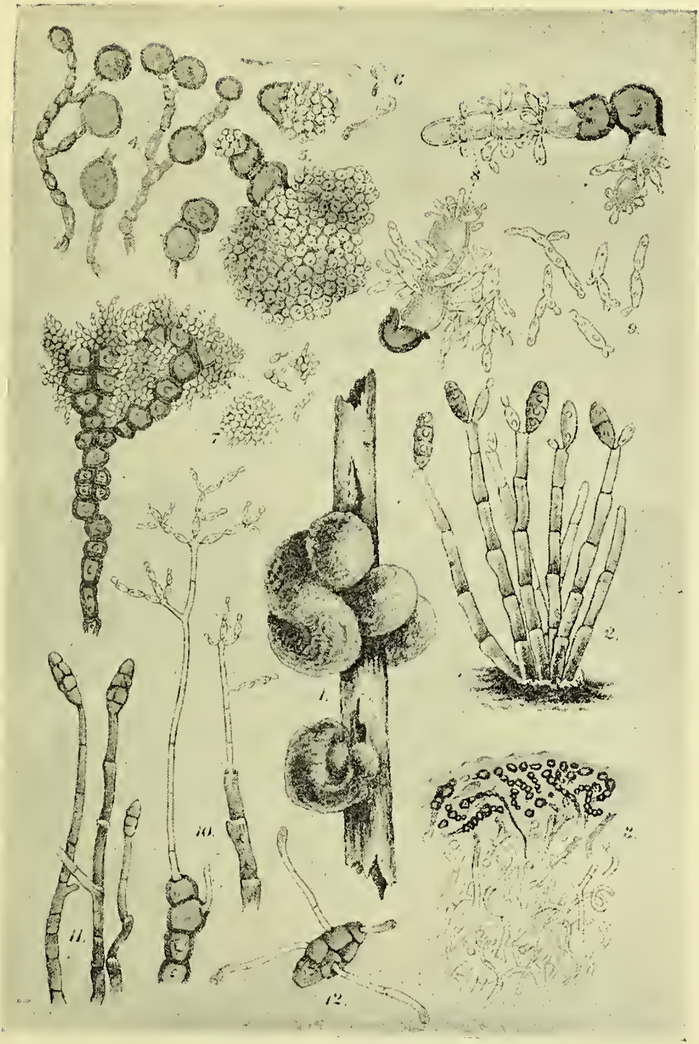
Hyphae pallid or brownish, densely coherent or fasciculate into a stem-like, erect structure. *Stilbeae.*

FIG. 131.—*Cladosporium fulvum*, a very destructive disease attacking the cultivated tomato. 1, under surface of a tomato leaf showing the reddish-brown patches formed by the crowded conidiophores; 2, a tuft of conidiophores bearing conidia. Fig. 1, about nat. size; fig. 2, highly mag.

Hyphae pallid or brownish, densely conglutinated into a wart-like mass (sporodochium), often springing from a compact stroma. *Tuberculariae.*

Mucedineae

In this family the conidiophores, although very often numerous and crowded in growth to form broadly expanded



For description see p. 400.

patches, never cohere together in fascicles to form a stem-like structure. Both hyphae and conidia are either colourless, or clearly and brightly coloured, never dingy brown, olive, or blackish.

The conidia may be either simple (unicellular) or variously cut up by septa into a varying number of cells.

Some genera as *Ramularia*, *Ovularia*, etc., are parasitic. Species of *Botrytis*, *Oidium*, etc., are now known to be conidial forms of ascigerous fungi. *Aspergillus glaucus* is the conidial form of *Eurotium herbariorum*.

FIG. 132.—*Cladosporium epiphyllum*. 1, portion of a branch of *Prunus japonica* bearing two masses of gum caused to accumulate by the fungus; 2, *Cladosporium* form of fruit; 3, section of a portion of the periphery of a black gum-mass, showing the hyphae of the *Cladosporium*; 4, dark-coloured tips of hyphae from the periphery of the gum-mass, bearing large, thick-walled, brown cells; 5, large thick-walled cells germinating in a nutrient solution in the absence of air, and producing yeast-like cells, which reproduce themselves by budding; 6, stray cells emitting germ-tubes, seen in the material described under 5; 7, micro-sclerotia germinating under conditions similar to those described under 5, and producing similar conidia; 8, large, brown, thick-walled cells germinating in a nutrient solution with free access of air, and producing the form of fruit known as *Dematium pullulans*; 9, conidium of the *Dematium* increasing by budding; 10, fragments of sporophores of *Cladosporium* producing a slender form of *Dematium pullulans*; 11, a form of *Macrosporium* often appearing on old canker spots caused by the *Cladosporium*: no genetic connection between the two could be established; 12, conidium of the *Macrosporium* germinating. Fig. 1, half nat. size; the remainder highly mag. (From *Kew Bulletin*.)

The full account of the research illustrated by this plate, and entitled 'Gummosis of Prunus Japonica,' is contained in the *Kew Bulletin*, 1899, p. 1.

Dematieae

Hyphae often forming a cottony or byssoid expansion of a dusky colour, rather rigid, not aggregated into definite fascicles or wart-like bodies. Both hyphae and conidia are typically dusky in colour, but in some cases the hyphae are almost hyaline and the conidia dusky; in other species the hyphae are dark and the conidia pale.

In some of the members the hyphae are completely buried in the matrix, and conidiophores very rudimentary, as in the genus *Torula*, where the superficial chains of conidia form blackish-olive stains on dead, herbaceous stems. In other genera, as *Dendryphium*, *Helminthosporium*, etc., the conidiophores are well developed, erect, and often more or less branched, bearing the conidia at the tips of the branches.

FIG. 133.—*Fusicladium pirinum*, a destructive parasite on pears. 1, fungus forming minutely velvety, dark-coloured patches on a pear leaf. The disease usually first appears on the leaves, from which the conidia are washed by rain, etc., on to the young fruit; 2, fungus forming scurfy patches, and causing cracking of the flesh of a pear; 3, conidiophores bearing conidia. Figs. 1 and 2, reduced; fig. 3, mag.

The conidia are produced singly or in chains, necklace-like (concatenate), and are sometimes one-celled and minute, as in *Coniosporium*; on the other hand, in *Macrosporium*, the conidia are comparatively very large and multicellular. The genus *Cercospora* is parasitic on living leaves.

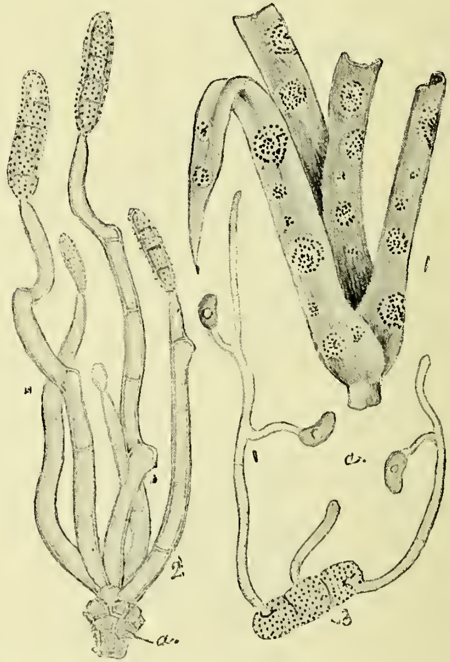


FIG. 134.—*Helminthosporium echinulatum*. 1, portion of a diseased carnation showing the pustules of fruit arranged in concentric circles; 2, small cluster of conidiophores bearing the large, minutely warted, septate conidia, borne singly at the tips of the conidiophores; 3, a conidium that has germinated in water: the germ-tubes bear short branchlets, each of which produces a small, dark-coloured, secondary conidium at its tip. Fig. 1, nearly nat. size; the remainder mag.

Species of *Alternaria*, *Macrosporium*, *Cladosporium*, etc., are suspected of being phases in the life-cycle of Sphaeriaceous fungi.

Stilbeae

The principal feature of this family consists in the fasciculate arrangement of a number of hyphae, which appear to be cemented together in a bundle to form a

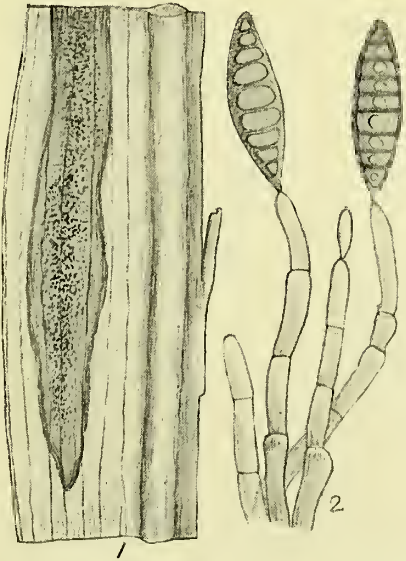


FIG. 135.—*Helminthosporium turcicum*, a fungus with simple conidiophores growing in clusters. Each conidiophore bears a single, many-celled conidium at its tip. 1, portion of a leaf of maize showing a large dark blotch formed by the fungus; 2, conidiophores bearing conidia. Fig. 1, nat. size; fig. 2, mag.

compound, upright stem; usually the tips of the component hyphae become free from each other near the apex and spread outwards, bearing either single or chains of conidia at the tips, the whole structure resembling a sheaf of wheat in miniature.

FIG. 136.—*Cercospora apii.* 1, a celery leaf attacked by the fungus; 2, conidiophores bearing long, slender, hyaline, septate conidia. Fig. 1, nat. size; fig. 2, highly mag.

Many of the species are yellow, some red, others pallid, some again are dingy and blackish.

Many of the species of *Isaria* are known to be conidial forms of ascigerous fungi belonging to the genus *Cordyceps*, which is remarkable for being parasitic on insects and spiders. Inoculation takes place during the life of the insect, which continues to live until the mycelium spreads in its interior and destroys all structure. The conidiophores of the *Isaria* form then appear on the surface of the body under the form of erect, feathery tufts, usually of a yellowish colour. Some time afterwards the ascigerous condition of the fungus appears on the surface, under the

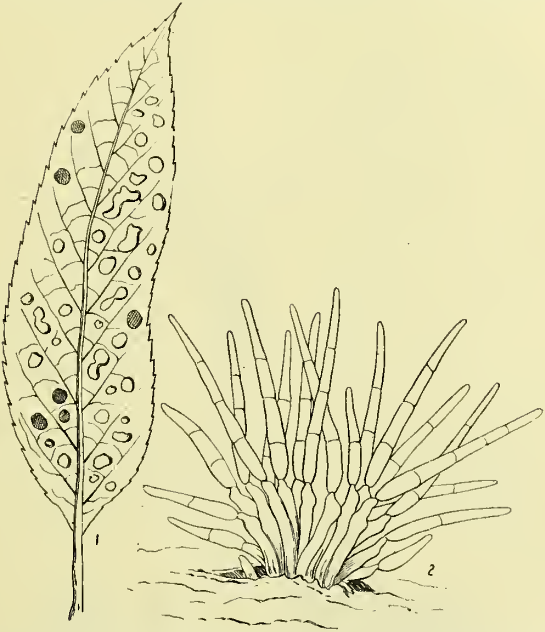


FIG. 137.—*Cercospora circumscissa*, a fungus whose conidial fruit consists of a single conidium produced at the tip of a short, unbranched conidiophore. 1, peach leaf showing blackened spots caused by the fungus. The small circular patches of leaf tissue killed by the fungus soon dry up and fall, leaving a number of holes in the leaf, hence the popular name of 'shot-hole fungus.' 2, a cluster of conidiophores bearing septate conidia. Fig. 1, nat. size; fig. 2, mag.

FIG. 138.—*Macrosporium nobile.* 1, portion of a carnation with numerous fruit pustules of the fungus; 2, two conidiophores, each bearing a muriformly septate conidium at its apex; 3, portion of a conidium germinating; 4, conidia of a species of *Fusarium*. Fig. 1, nat. size; remainder mag.

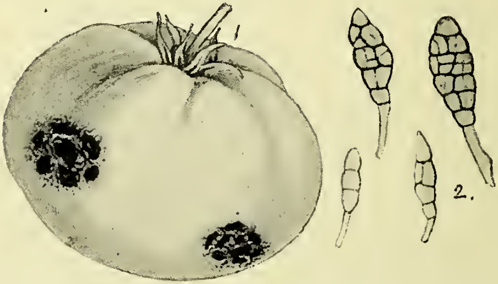


FIG. 139.—*Macrosporium tomato,* a destructive tomato disease. 1, a tomato showing two groups of fruit pustules; 2, muriformly septate conidia in various stages of development. The transverse septa are first formed, the vertical or oblique septa appearing at a later date. Fig. 1, nat. size; fig. 2, mag.

form of erect, club-shaped bodies of a dingy brown or sometimes bright red colour. *Cordyceps militaris*, having a bright orange-red club, is not uncommon on the larvae of insects in this country.

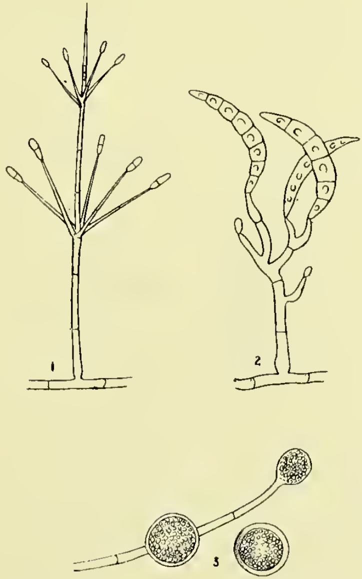


FIG. 140.—*Fusarium lycopersici.* This fungus has two distinct conidial stages: no higher form of fruit is as yet known. 1, *Diplocadium* stage: the erect conidiophores bear two or three whorls of branchlets, each bearing a conidium at its tip; 2, *Fusarium* stage: the conidiophores are short, and bear a few short branchlets near the apex, each of which bears a hyaline, septate, sickle-shaped conidium; 3, chlamydospores which become thick-walled and act as resting-spores: these are produced interstitially or terminal on the mycelium of the *Fusarium* stage, permeating the matrix. All figs. highly mag.

Tubercularieae

In this family the hyphae are densely compacted to form a hard, subglobose, wart-like body, which is erumpent or bursts through the matrix, below the surface of which it is developed. The bright coral-red warts of *Tubercularia cinnabarina*, so abundant on dead twigs, branches, etc., is a good example of the general structure characteristic of the family.

FIG. 141.—*Fusarium heterosporum*, a parasite attacking ears of barley and other cereals, destroying the grain. 1, portion of an ear of rye showing diseased grains; 2, diseased grains shown singly; 3, section of portion of a diseased grain showing clusters of sporophores on the surface: these sporophores, along with the conidia, form pinkish orange, somewhat gelatinous masses when moist; 4, sickle-shaped, multiseptate conidia. Fig. 1, nat. size; remainder mag.

Many species are destructive parasites. Some of the forms of *Tubercularia* are known to be conidial forms of the ascigerous genus *Nectria*. Forms of *Fusarium* are also known to be connected with species of *Nectria*. Species of the genus *Tuberculina* are parasites on the Uredo and Aecidium stages of various Uredines, which are themselves parasites on the higher plants.

Allescher, 'Fungi Imperfecti,' *Rabenh. Krypt.-Flora, Pilze*, 1, Abt. 6 and 7 (1901-3).

Engler and Prantl, 'Fungi Imperfecti,' *Pflanzenfam.*, 1, Abt. 1** (1900).

Massee, 'Hyphomycetes (British),' *Brit. Fungus Flora*, 3 (1893).

Saccardo, 'Sphaeropsideae and Melanconicae,' *Syll. Fung.*, 3 (1884).

Saccardo, 'Hyphomycetes,' *Syll. Fung.*, 4 (1886).

ADDENDA

The following are supplementary to subjects noticed in this book, and have appeared too late for incorporation in the body of the work :—

Enzymes present in Polyporus squamosus

From an anatomical study of wood undergoing decay through the agency of *Polyporus squamosus*, evidence of the action of enzymes was observed. Buller, who has made an investigation of the subject, has succeeded in proving the presence in the fungus of laccase, tyrosinase, amylase, emulsive, a protease, lipase, rennetase, and 'coagulase.' A study of the destruction of the wood of the Sycamore (*Acer pseudoplatanus*) points to the conclusion that the mycelium produces cytase and possibly also a hadromase; thus the fungus produced eight or nine enzymes, perhaps a greater number than has been found in any other organism. However, Bourquelot has proved the existence of seven enzymes in *Aspergillus*, namely, invertase, maltase, trehalse, inulase, emulsin, diastase, and trypsin.

A portion of the fungus cut into thin slices and carefully dried at a temperature of about 80° C., after being preserved for nine months, showed that the extract was as active as that obtained from fresh material. Thus milk was clotted in fifteen minutes; an 0·2 per cent. of Lintner's starch solution underwent complete hydrolysis in three hours, and gelatine was liquefied in about the same time as with fresh material. Such material is therefore well suited for experiments by students in the laboratory.

Buller, *Ann. Bot.*, 20, p. 49 (1906).
Bourquelot, *Bull. Soc. Myc.*, 1893, p. 231.

An endophytic Member of the Erysiphaceae

A brief account of the endophytic nature of the conidial form of *Erysiphe taurica*, as noted by Salmon, has already been given. This author has now published a fuller account, and points out that *E. taurica*, during its conidial stage, differs from all other known Erysiphaceae in two main points: the complete absence during this stage of any mycelium on the surface of the leaf, and the presence of conidiophores emerging singly or in bundles through the stomata.

A further peculiarity is presented by the conidiophores which are frequently found to be branched, a character not previously known to occur in the family.

In the later stages of the conidial condition mycelial hyphae emerge in great numbers through the stomata, and form an external mycelium on the surface of the leaf preparatory to the formation of perithecia.

On account of the peculiarities enumerated, Salmon considers that *E. taurica* differs generically from the other members of the Erysiphaceae, and proposes the generic name *Oidiopsis*—a name previously given to the conidial form of *E. taurica*—for its reception.

A new sub-family is also proposed for the reception of this new genus, called Oidiopsideae, characterised as follows :—

Mycelium at first wholly endophytic, producing conidiophores sent up through the stomata; perithecia produced on the hyphae of a superficial mycelium originating from the endophytic mycelium.

Salmon, *Ann. Bot.*, 20, p. 1 (1906).

Sexuality of the Uredineae

A brief summary has been given of Blackman's investigations on a peculiar process observed in *Phragmidium violaceum*, where the nucleus of an ordinary vegetative cell migrates into a special 'fertile cell,' which then develops and gives origin to a chain of binucleate aecidiospores. The fertile cell was considered to be a female cell, and its union with the vegetative cell as a 'reduced sexual process,' in which the vegetative cell replaces the now functionless spermatium.

Christman, as already explained, also investigated other species of the Uredineae, *Phragmidium speciosum*, etc., and found that in some species two of Blackman's uninucleate 'fertile cells' conjugate in pairs; from such fusions binucleate cells are produced, which give origin to chains of aecidiospores.

Christman differs from Blackman in considering the conjugating cells as ordinary undifferentiated gametes.

Blackman, however, does not agree to this view, and supports his previous statement as follows:—

'If, however, the view be accepted that the fertile cells of *P. violaceum* represent female gametes, which are now fertilised by vegetative cells instead of by male cells (the now functionless spermatia), it follows that the cells which fuse in *P. speciosum*—since the structure and development of the aecidium is exactly the same in the two cases—also represent *female cells which now conjugate in pairs.* By such a very simple interpretation the two processes are reduced to a common term. The two species of *Phragmidium* are then seen to be merely two different methods of dealing with the same problem—fertilisation in the absence of the male cell. In the one case the male cell is replaced by a vegetative cell; in the other by another female cell.

'If, on the other hand, Christman's view of the behaviour of *P. speciosum* be accepted, it must also apply to *P. violaceum*, and it leads to the unsatisfactory conclusion that the fertile cells here also represent undifferentiated gametes, which for some obscure reason have given up fusing in pairs, and now fuse with vegetative cells instead.

'The view put forward above obviously explains the relation of the two processes throughout the group, and has the further advantage of giving a reasonable explanation of the structure and occurrence of the spermatia, which in Christman's view are left out of account.

'That the conjugation of female gametes may take place in the absence of the appropriate male cell is shown clearly by the author's studies on *Humaria granulata*, where, in the absence of the antheridium, the female nuclei of the ascogonium fuse in pairs.'

Further investigations by Blackman and Fraser have resulted in the discovery, in other members of the Uredineae, of the conjugation of cells after the manner described by Blackman and Christman respectively, and the authors consider that these two methods are simply variants of a method of *reduced* fertilisation by spermatia.

Blackman and Fraser, *Ann. Bot.*, 20, p. 35 (1906).

,, ,, 'On the Sexuality and Development of the Ascocarp in *Humaria granulata*,' *Proc. Roy. Soc.*, ser. B., 77 (1906).

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