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TO

ROLAND THAXTER

PREFACE TO THE AMERICAN EDITION

In presenting this translation and revision of Gäumann's "Comparative Morphology of Fungi" to the American public, it is desirable to state the principles which have guided in this work. An attempt has been made to secure a free translation, conveying the ideas expressed in as idiomatic English as possible rather than to follow the German closely. Whenever any ambiguity has appeared, the original papers have been consulted and followed. The theoretical discussions of phylogeny have been preserved, even though it is impossible for me to agree with some of the conclusions. The rearrangement of the orders is made with the author's approval, since the arrangement in the German edition followed the traditional arrangement rather than expressed the author's personal views. This arrangement being less traditional in America, the need for its preservation seemed less. This rearrangement has necessitated rewriting most of the orders of the Basidiomycetes, except the rusts and smuts.

Throughout the book, such new literature (1925–1927) as I have found, has been incorporated without special mention or change of the discussion of the phylogeny. In a few cases, the abundant new literature has necessitated a complete rewriting of the discussion of the group in question. That of the Basioboleae was rewritten in the light of Miss Levisohn's paper and that of the Elaphomycetaceae as a result of my own observations. The papers of Wehmeyer on the stromatic Sphaeriales necessitated a complete revision of the Diatrypaceae and Diaporthaceae. Two new volumes of Thaxter's monograph of the Laboulbeniales, and Gäumann's misinterpretation of some of Thaxter's previous statements and figures, necessitated a new discussion of that order. Gäumann's phylogenetic discussion and my criticism of his statements have been relegated to smaller type at the close of the order, leaving the main discussion a statement of facts. The papers of Burt on the Thelephoraceae (*sensu latiore*) have opened up a wealth of new forms, here dealt with in the Corticiaceae, Cyphellaceae, Tremellaceae and Septobasidiaceae. The discussion of the Radulaceae (Hydnaceae of most authors) is based partly on Banker's excellent papers and partly on my own observations. The treatment of the Gasteromycetes (including the Plectobasidiales, the Podaxaceae and the Secotiaceae of Gäumann's treatment), except that of the Clathraceae and Phallaceae, has been completely rewritten in the light of recent ontogenetic papers and my own observations of the last decade, and I assume full responsibility for

any opinions expressed therein. The papers of Faull on the Pucciniastreae and of B. O. Dodge on the rusts of *Rubus* have necessitated extensive alterations in the Uredinales.

Personally, I feel too much weight has been attached to the differences between the sticho- and chiastobasidia; hence I am not at all in sympathy with the segregation of the Cantharellales as a separate order. There are no other constant morphological characters to separate the two types, but I have retained this segregation in a less exaggerated form as presenting a viewpoint which should stimulate further work to prove its truth or falsity.

Obvious errors in synonymy have been corrected, with the first mention of a species usually followed by parentheses containing synonyms used in the original papers. To save space, authorities for names have been omitted in the body of the text and given in full, as accurately as I have been able to determine them, in the index. The bibliography has been assembled in a single chapter at the end of the book, again to save space, and has been verified insofar as the books and periodicals were readily available.

In conclusion, I wish to express my gratitude to the following persons who have kindly loaned me unpublished manuscripts for inclusion in this edition: Professor J. H. Faull of Toronto, for his paper on the Pucciniastreae delivered at the International Congress at Ithaca, 1926; Dr. C. L. Shear and Dr. B. O. Dodge for their paper on *Neurospora*, delivered at the winter meeting of the Botanical Society of America at Philadelphia, 1926; Dr. L. E. Wehmeyer for his unpublished papers on the Diaporthaceae. Dr. Margaret B. Church kindly read the discussion of the Aspergillaceae and Dr. Roland Thaxter that of the Laboulbeniales, criticizing and adding new information as the result of his unpublished observations on this group. I deeply regret that Dr. Gäumann's illness has prevented his collaboration in this revision.

Dr. Thaxter has kindly furnished the drawings for Figures 253 to 261, Figure 230 is reproduced from Heald's *Manual of Plant Diseases*, Figure 234,2 from an unpublished drawing by Louis C. C. Krieger in the Farlow Library, the rest being the cuts used in the German edition, through the kindness of the publisher, Gustav Fischer of Jena. Finally, I wish to acknowledge my gratitude to my wife for her cooperation in preparing the manuscript for the press and reading the proof.

C. W. DODGE.

CAMBRIDGE, MASSACHUSETTS,
December 1, 1927.

PREFACE TO THE GERMAN EDITION

By the introduction of cytological methods of investigation to mycology, we have arrived at a much clearer conception of many of the problems of comparative morphology. In general, the classification of fungi has remained the same, but its interpretation has been strengthened and deepened in many ways. The task of this book is to present these conceptions in the most concise form. To my teacher, Eduard Fischer, Professor of Botany in Bern, I dedicate it as a token of my gratitude. Many of the ideas presented here, I owe to his lectures and conversation.

In the introductory chapters, the most important points of view and the basic forms are briefly discussed, assuming a knowledge of a textbook similar in content to that of Strasburger. This first part contains a brief summary of present knowledge. The remainder of the book describes modifications of the basic forms in the different groups. In order to shorten this presentation, we have dispensed with a discussion of the historical background of our knowledge. To anyone interested in this aspect of the question, we may recommend the excellent work of Vuillemin (1912). I have attempted, however, to present the divergent conceptions of various authors with the data on which they are based, and to deal with them justly. In order to facilitate special studies, I have included many references to recent works which contain summaries of the older literature.

I would like here to express my thanks to all those who have aided me with information, material from their herbaria and libraries, by copies of their works, or permission to use their figures. I wish especially to thank my wife for her assistance in redrawing the figures and the artist, E. Tobler of Zürich, who provided some habit sketches.

I am greatly indebted to the publisher, Dr. Gustav Fischer, who readily agreed to all my proposals for the preparation of this book.

As all such books, this contains many omissions and errors; I admit them willingly and will be grateful to have any pointed out so that they may later be corrected.

Dr. Ernst Gäumann,
Botanist, Swiss Agricultural Experiment Station,
Docent, Federal Technical High School.

Oerlikon-Zürich,
October, 1925.

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COMPARATIVE MORPHOLOGY OF FUNGI

CHAPTER I

INTRODUCTION

There are two distinct phases in the cytological development of sexually reproducing organisms, the **haploid phase** with the single or x number of chromosomes, and the **diploid phase** with the double or $2x$ number. The former ends with fertilization, the latter with meiosis.

A morphological change in the organism occurs parallel and in the same rhythm with this change in nuclear condition and is apparently correlated with it. Certain specialized cells or groups of cells which usually produce the characteristic organs of fertilization, always appear at the transition from haploid to diploid phase, while meiosis occurs at the transition from diploid to haploid phase. According to their corresponding nuclear phase, these cells or groups of cells are called **haplont** (haploid soma) and **diplont** (diploid soma). In an ideal case this cytological and morphological change of phase may be represented by the following diagram:

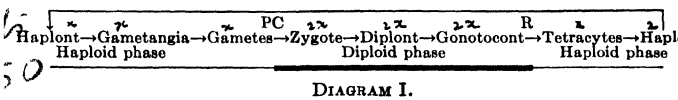


DIAGRAM I.

Gametangia containing gametes are formed on the haplont. **Plasmogamy** (a fusion between two sexual cells) which is followed sooner or later by **caryogamy** (a fusion of two sexual nuclei) takes place between pairs of gametes. These two processes are indicated as P and C in the above diagram. The product of fertilization is called a **zygote** as long as it remains unicellular; it develops into a diplont which forms **gonotoconts** (organs in which meiosis occurs). The products of meiosis, in so far as they are spores, are called **tetracytes** and develop into new haplonts. In the ideal case, haploid and diploid phases show a similar structure: haplont corresponds to diplont, gametangium to gonotocont, gamete to tetracyte. Fertilization and meiosis are the cardinal points in the life cycle, indicated in the foregoing diagram by means of the

appropriate letters above. The haploid phase is underlined by a narrow line, the diploid by a broad one.

The extent of development of haplont and diplont are very different for different groups of organisms. On one extreme the **thallus** (vegetative body) is haploid and the diplont is reduced to a zygote incapable of separate existence. There are many intermediate cases to the other extreme in which the thallus is diploid and the haplont is reduced to a few cells parasitic on the diplont. An intermediate condition is reached in forms in which haplont and diplont are two distinct thalli. Haplont and diplont here follow each other as two morphologically different generations. In this case we have **alternation of generations.** The haploid generation is called the **gametophyte,** the diploid, the **sporophyte.** These relations are further complicated in certain cases where an organism regularly passes through several different, morphologically distinct stages of development within the same nuclear phase, *e.g.*, the protonema and moss plant in the haploid phase of mosses and the larval, pupal and imago in the diploid phase of insects (Maire, 1900, 1902; Lotsy, 1907; Buder, 1916; Goeldi and E. Fischer, 1917; Kylin, 1917; E. Fischer, 1919; Svedelius, 1921, 1927).

These different rhythms are not so strongly fixed in the fungi as in higher organisms. They have been modified and have displaced one another because of parthenogenesis, apogamy, apomeiosis, because of environmental changes or because of retardation or hindrance of fertilization or of meiosis. Since the comparison of these rhythms makes a desirable scheme in which to arrange morphological facts, it will be given the chief emphasis in this book. It is the aim of comparative morphology to follow the cytological development of the life cycle and to examine the ontogeny of thalli and fructifications by comparing them in both phases.

CHAPTER II

THE THALLUS

The thallus (vegetative body) is naked and at times amoeboid in the simplest families of fungi; in the rest, it is surrounded by a cell wall and is usually in the form of septate hyphae. Under certain conditions of nutrition, as in solutions of small nutritive value, the hyphae grow by sprouting, in which process small protuberances are formed which enlarge, round off and are **abjointed** (cut off by a septum) from the mother cell, then continue to increase in size and sooner or later separate from the original groups of cells (Fig. 1, *a*, *e*, *f*). These are called **sprout cells** or occasionally, and less correctly, sprout conidia. In certain groups they form the only type of thallus known. Under unfavorable conditions of growth, the protoplasm contracts, rounds up and secretes a special, thick membrane; these resting cells are called **gemmae.** Under suitable conditions, they grow to normal thalli.

In some groups the hyphal wall gives the chitin reaction, in others that of cellulose; in fructifications and resting cells it is usually strengthened by mineral incrustations, by secretions of resins, etc. At first it forms a hyaline membrane which becomes thicker, is further differentiated by secretions and deposits and usually colored by pigment deposits. An unquestioned relation between the fundaments of the wall, especially the septum, and mitosis has been proved only in a few cases; an especially characteristic example occurs in ascospore formation. As a rule the wall is gradually differentiated from the cytoplasm without nuclear aid, in endogenous spore formation simultaneous with cell elongation, in septal formation by **furrowing** (ring-like thickening of the walls like an iris diaphragm). For the maintenance of intercellular communication, the septa are usually pierced by a few openings through which pass protoplasmic threads

In rapid growth, septal formation may be delayed, later it is made up for by simultaneous or successive septal formation. In certain groups, as in the Siphonales among the algae, the septa are wholly suppressed; the whole thallus is then a single ramose, multinuclear sac which becomes septate only in the formation of reproductive organs, in conditions of poor nutrition and in age. Since these sacs contain numerous undifferentiated energids, they are called **coenocytic** (polyenergid).

The individual hyphae usually creep about and are intertwined in felt-like masses. Such a group of hyphae is called the **mycelium.** In

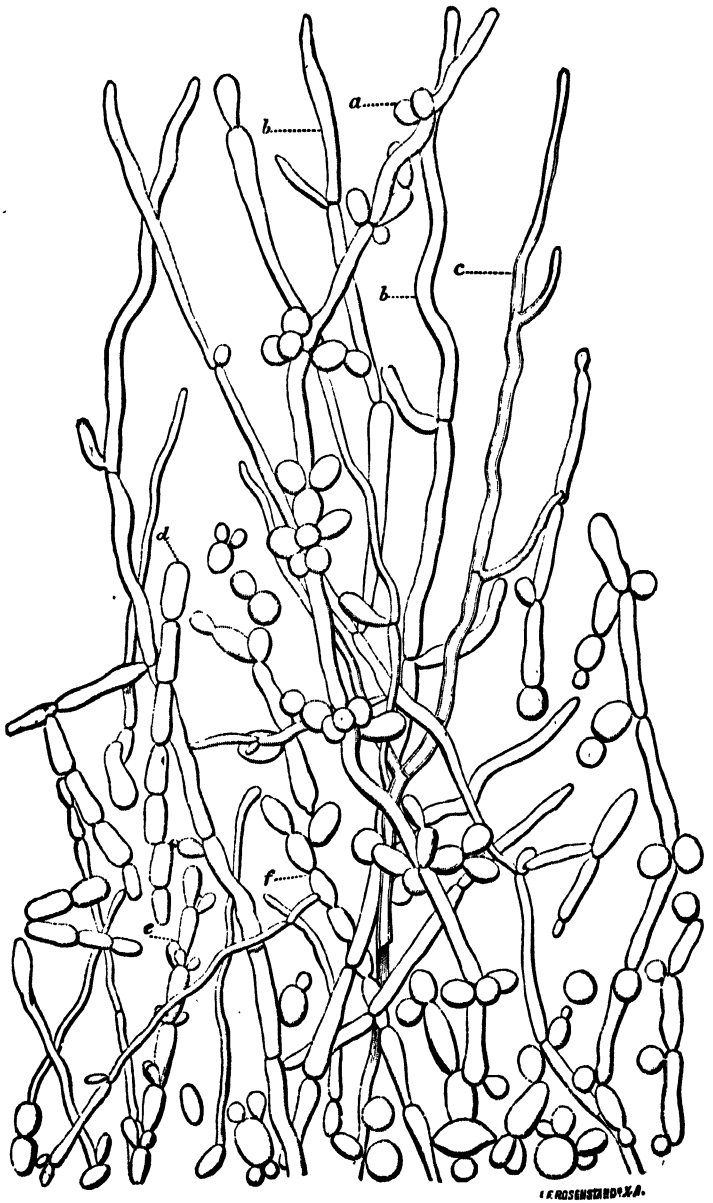


FIG. 1.—*Monilia candida.* Formation of sprout cells. *b*, *c*, typical hyphae; *a*, *e*, *f*, sprout cells; *d*, oidia. (× 1,000; *after Hansen.*)

ectoparasitic, less often in parasitic, forms it may cling fast to the substrate by holdfasts known as **appressoria** (Fig. 215, 2). Usually it is able to absorb food over its whole surface; yet for the better fulfilment of this function, special hyphae or hyphal branches are developed in saprophytic forms as **rhizoids** (Fig. 55, 1) and in parasitic forms, **haustoria** (Fig. 120). Occasionally these structures function as holdfasts as well as food absorbers. It is still an open question whether the haustorium is a normal organ or whether it is not more often restricted in growth and deformed by the action of the host cells.

In many cases the hyphae grow together in groups, intertwine, adhere and form a thick tissue which is called **plectenchyma.** If the single hyphal elements are still recognizable as such (Fig. 2, *b*), they are called

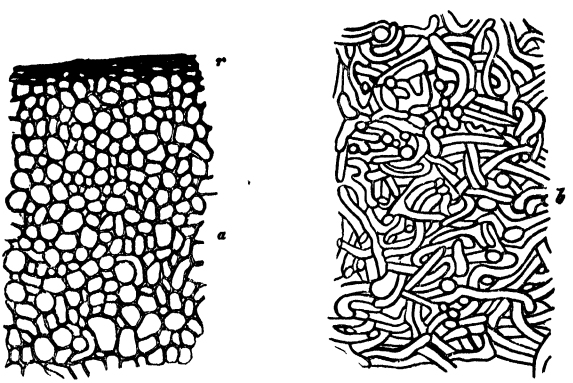


FIG. 2.—*Claviceps purpurea.* Section through a sclerotium. *a*, peripheral layer of pseudoparenchyma; *b*, core tissue of prosenchyma; *r*, rind. (× 360; *after Tavel.*)

prosoplectenchyma or **prosenchyma**; if the hyphae have lost their individuality so that they lie beside each other (in sections) with the cells appearing isodiametric and continuous, as in the parenchyma of higher plants (Fig. 2, *a*), they are called paraplectenchyma or **pseudoparenchyma.**

In **sclerotia** the plectenchyma appears tuberiform with a firmer pseudoparenchymatic rind and a looser prosenchymatic core. This structure serves to carry the organism over unfavorable conditions of growth and, with the return of normal conditions, germinates to the usual mycelium or to a fructification. **Bulbils** are small sclerotia formed of a few layers of cells, and are often present in large numbers.

Rhizomorphs indicate a further step in the development of plectenchyma. They arise chiefly from parallel hyphae and often have a definite apical growth from an apical meristem, as the root tips of cormophytes. Under suitable conditions, they may again spread out in sheets of myce-

lium. In the higher forms, a dark, thick, irregularly intertwined rind and a loose, white core are differentiated from parallel hyphae. They serve, as will be shown in the Basidiomycetes, chiefly for transport of food.

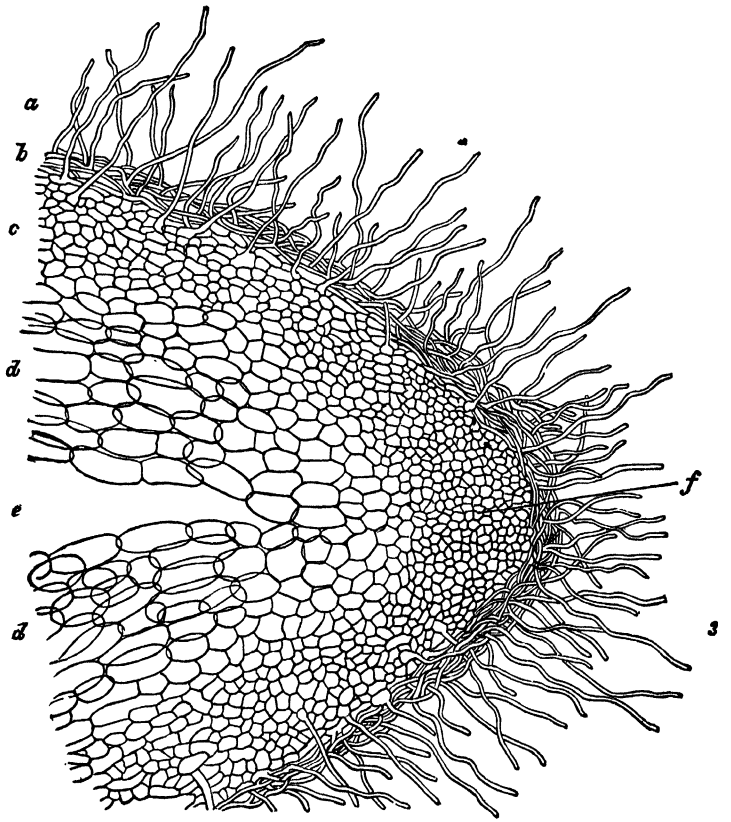


FIG. 3.—*Armillaria mellea.* Longitudinal section of tip of rhizomorph. *a*, loose hyphae; *b*, gelatinous, loosely interwoven hyphal layer; *c*, *d*, core layers; *e*, central cavity; *f*, apical meristem. (× 300; *after Hartig.*)

Occasionally the conducting function becomes less evident and they attain a more sclerotic character.

The plectenchyma attains its highest development in fructifications where the differentiation is reminiscent of the cormophytes.

CHAPTER III

FRUCTIFICATIONS

In most fungi, at a definite age and under favorable conditions of nourishment, the mycelium proceeds to the formation of fructifications. In the simplest unicellular families, as in the protozoa, the whole (unicellular) thallus becomes transformed into a fructification. These forms are called **holocarpic.** The thallus (vegetative condition) and the fructification (reproductive condition) of the same individual show in some cases two successive phases of development; in other cases these phases are concealed and are only recognizable as different because of their functions.

In the other fungi, the thallus and fructification are separate from each other both in time and space; only a portion of the thallus is used for the formation of the fructification, while the rest remains to serve its original vegetative function. These forms are called **eucarpic.**

The products of the reproductive processes are chiefly spores. Spores are characteristically formed cells or groups of cells which separate from the mother plant and may grow independently to new individuals. They serve either for propagation (multiplication and dispersal) or overwintering (as hypnospores or resting spores).

In the simplest case, they arise by the separation of hyphal cells (Fig. 263, 1), which grow into new hyphae. These individual cells are called **oidia** and are homologous to the cells of a sprout hypha, only the latter arise by sprouting rather than by the breaking up of a hypha.



FIG. 4. — *Saprolegnia mixta.* Zoosporangium discharging zoospores, S^2. (*After Klebs.*)

From oidia, there is an imperceptible transition to definite spores, characteristic in form, color or sculpturing of the wall. In many cases they are cut off directly from the ordinary hyphae; in other cases they arise on special sporophores. If these sporophores form the spores endogenously from particular sporogenous cells, **sporangia,** they are called **sporangiophores,** and the spores, if they are naked and motile, are called **zoospores** (Fig. 4), or, if they are enclosed and non-motile, **sporangiospores** (Fig. 5, *sp*). If the sporophores cut off their spores exogenously,

they are called **conidiophores** and the spores themselves **conidia** (Fig. 6). A special type of thick-walled conidium is called a **chlamydospore** or, in the resting state of the mycelium, a **gemma.** Chlamydospores have an entirely different morphological significance in different orders, as we shall see in the course of this book.

In the higher fungi, the hyphae forming the conidiophores show a tendency to come together into groups or fructifications. When these groups have the form of fascicles, they are called **coremia;** if they form widespread cushions, they are called **sporodochia** in saprophytes and **acervuli** in parasites; the tissue from which they arise is known as their **stroma.** If the conidial hyphae join in groups of plectenchymatous structures in whose interior they cut off their spores, these structures are

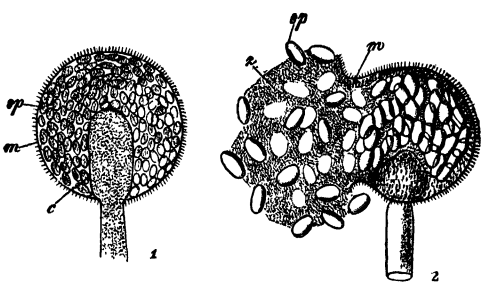


FIG. 5.—*Mucor Mucedo.* 1. Sporangium with sporangial wall, *m*; sporangiospores, *sp*; and columella, *c*. 2. Sporangium rupturing intermediate substance, *z*. (*After Brefeld.*)

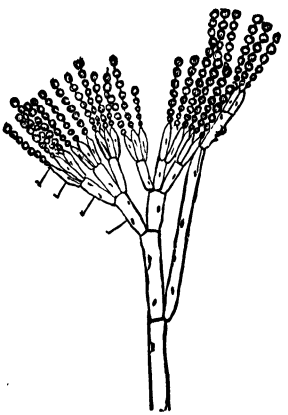


FIG. 6.—*Penicillium crustaceum.* Conidiophores. *St*, sterigma; *Ph*, phialide; *M*, metula; *A*, primary branch. (*After Strasburger.*)

called **pycnia** (pycnidia) and the conidia themselves (for better differentiation from other conidia) are called **pycnospores,** pycnidiospores or stylospores. In case the pycnia arise by growth and division of a single portion of a hypha with the aid of neighboring branches of the same hypha, the method is called **meristogenous.** If they arise by the intertwining and coiling of hyphae of different origin, however, their method is called **symphyogenous.** These distinctions have a limited value as these types pass into each other and are at times found in the same species, *e.g.*, the pycnia of *Phoma conidiogena* are formed entirely meristogenously with poor media and more symphyogenously with good media (Schnegg, 1915; Kempton, 1919; B. O. Dodge, 1923a).

These different spore forms—oidia, gemmae, conidia, etc.—may be formed on a suitable part of the haplont (rarely also on the diplont in

the Basidiomycetes) as soon as conditions of nutrition suffice. A limitation exists only in so far as the isolated sporophores usually occur earlier than the corresponding fructification. Where several spore forms occur in the same species, it is called polymorphic.

Another group of spore forms is not primarily dependent for its initiation on the conditions of nutrition but on the rhythm of the change of nuclear condition: either because their formation follows fertilization or because meiosis generally takes place in the sporophore. In the first

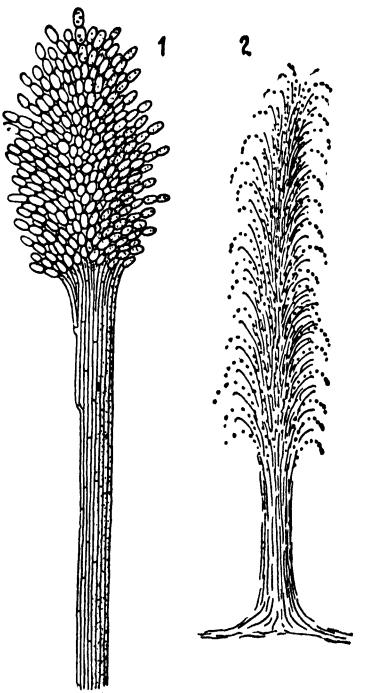


FIG. 7.—Coremia. 1. *Stysanus thyrsoideus*. 2. *Scopulariopsis* (*Acaulium*) *nigra*. (1 × 220; 2 × 40; *after Sopp*, 1912.)

case, they are connected with the beginning, in the latter with the end of the diploid phase.

In the first case they are recognizable morphologically since they show encysted zygotes (the products of the sexual act); biologically they usually develop as hypnospores. According to the morphological position of the cells which copulate, their morphological significance and name varies, as we shall see in individual cases.

In the second case, they are morphologically recognizable since they form tetracytes (as daughter cells of gonotoconts). Apparently, since

they are products of meiosis, they have become constant in number, which is usually fixed at 8 or 4; biologically, in the higher forms they are hypnospores. If the sporogenous cells which serve as gonotoconts form their spores endogenously through free cell formation, they are called **asci** and the spores **ascospores** (Fig. 81); if they are formed exogenously by cutting off spores, they are called **basidia** and their spores, **basidiospores** (Fig. 265, 7 to 14).

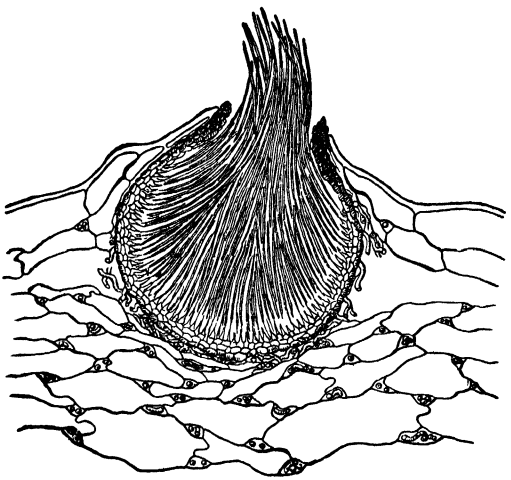


FIG. 8.—*Septoria*. Pycnium. (*After Klebahn.*)

Both these sporophore types functioning as gonotoconts show the same collectivistic tendency as the sporophores of the haplont. They collect in groups or in layers on which they stand beside each other in palisades which are called **hymenia.** The hymenia develop in typical gymnocarpous or angiocarpous fructifications whose structure is always highly differentiated. As only in these highest groups do the gonotoconts become sporophores and especially as the gonotocont fructifications are the only ones visible to the naked eye, the gonotoconts of the groups in question (asci and basidia) are called the **perfect forms,** the other spore forms are called **imperfect** or **secondary spore forms.**

CHAPTER IV

SEXUAL ORGANS AND SEXUALITY

The sexual function involves two processes: (*a*) **fertilization,** *i.e.*, a fusion of two nuclei, periodically recurring in the course of development and setting free specific stimuli for development; and (*b*) **meiosis,** *i.e.*, a return to the single chromosome number. This rotation (haplont–fertilization–diplont–meiosis) forms the changes of nuclear condition mentioned in the introduction. A few fungi seem to exist without a change of nuclear condition; they seem to be accustomed to living an unlimited number of "generations" without reconstruction of their nuclei and to propagate themselves by imperfect stages only. These fungi with incomplete, or incompletely known, life cycles are called Fungi Imperfecti or Deuteromycetes.

The fungi with complete life cycles are divided, as are all other sexual organisms, into monoecious (bisexual or hermaphroditic) and dioecious forms. In contrast to the higher plants, in these fungi the question of the division of sexes is limited to the haplonts, *i.e.*, the thallus, and the monoecious forms are called **homothallic** or neutral and the dioecious forms, **heterothallic.** The former are indicated as ±, the latter as + or −. The + and − mycelia of the latter group may be distinguished from each other only dynamically (*i.e.*, only physiologically, as a result of their sexual tendencies) or morphologically (*e.g.*, in growth form, sexual dimorphism).

The process of fertilization in fungi, as in algae and protozoa, takes place in many ways (Winkler, 1908; Hartmann, 1909, 1918; Guillermond, 1913; Ernst, 1918). The simplest normal type of fertilization, when two spatially separated, not closely related sexual cells fuse to form a new entity, is called **amphimixis.**

If these sexual cells arise as daughter cells of a characteristic mother cell and are themselves characteristically formed, they are called **gametes** and the mother cells **gametangia** (Fig. 11, 13 to 15). The copulation of two specific gametes of this type is called **merogamy.** If the gametes are equivalent to each other, the copulation is called **isogamous,** if the gametes are different, their copulation is **heterogamous.** If in the latter case one gamete is motile, the other non-motile, the former is called **sperm** (spermatozoid) and the latter, **egg** (Fig. 34). In the lower fungi, the gametes are doubtlessly derived from zoospores which are weakened by under-

nourishment and are no longer capable of independent development. They proceed in pairs to autophagy, and the product of their fusion acquires a new specific ability for development.

Under the influence of tendencies which will be brought out in the course of the discussion, the individualization of the gametes in the gametangia ceases at a low stage and the contents of the gametangia remain **polyenergid.** Thereby the original copulation of gametes is suppressed and replaced by many secondary processes which compensate for the loss of the original merogamy. All these secondary processes of fertilization are called **deuterogamy** (secondary pairing). In this category fall the processes of the higher algae and phanerogams (except the lower gymnosperms) while in the animal kingdom the primitive merogamy has persisted up to the highest vertebrates.

In deuterogamy the gametangia assume the function of their daughter cells, the gametes, and cause their coenocytic content to fuse without further differentiation (Fig. 50). A sexual act occurs between two sexual organs instead of between sexual cells, and sexual attraction passes from the latter to the former. This type is called **gametangial copulation.** It assumes close contact between two gametangia and has a biologically obvious consequence that one gametangium can fertilize only one other which must be located directly next to it; but it has the obvious advantage that it no longer remains to chance whether the two gametes find each other, for the gametangia provide that their nuclei reach each other and fuse. Viewed caryologically, the effectiveness of gametangial copulation becomes greater since most of the nuclei of both succeed in their activity and consequently the number of zygote nuclei increases; viewed numerically, only a small fraction are effective, for the fate of whole gametangia depend on the occurrence or non-occurrence of a single sexual act and only one very strong coenocytic zygote results instead of many smaller unicellular zygotes. There is a special advantage for the gametangium, since at its maturity it is no longer dependent on a definite medium for the copulation of its gametes and consequently it has made possible an easier transition from water to land habitats, and to parasitism in the interior of other plants. Whether gametangia are formed on special branches or whether these branches as a whole complete the act of fertilization, they are called copulation branches. In the case of heterogamy they are distinguished as **antheridium** (male) and **oogonium, archicarp** or **ascogonium** (female).

In the holocarpic forms, gametangial copulation naturally leads to the fusion of whole individuals (Fig. 26, 4 and 5) and is equivalent in a certain sense to self annihilation. This special case of gametangial copulation, in which two mature individuals copulate, is called **hologamy.** In the fungi, in contrast to certain flagellates, it has doubtlessly arisen secondarily from merogamy.

In the higher Ascomycetes, for reasons still unknown, the fundaments of the antheridium are gradually reduced; thereby cross-fertilization generally ceases and is replaced by self-fertilization, *i.e.*, a new group of deuterogamous processes between daughter cells of the same mother cell or between the nuclei of the same cell which are included in the term **automixis.**

Automixis is represented in the fungi by two forms: parthenogamy and autogamy. **Parthenogamy** (parthenomixis of Winkler) is fertilization which takes place between two female cells, *i.e.*, in the fungi usually between two cells of the archicarp (Fig. 227). In certain forms this parthenogamic fusion of two specialized cells is suppressed and replaced by pairing of nuclei within a single polyenergid cell of the archicarp (Fig. 229). This automictic fertilization within a cell is called **autogamy.**

From these forms in which the sexual organs (or in any case the female organ) are apparently still typical in form, but no longer functional and serving only as the site of automictic processes, there is a series of intermediate stages to the other extreme in which the sexual organs are entirely suppressed, the sexual processes occurring outside in the thallus between any two sexually differentiated vegetative cells (Fig. 266, 1). The latter process is called **pseudomixis** (pseudogamy of Hartmann). Since the copulating cells are not morphologically distinguished from other vegetative cells and since only the release of specific developmental stimuli, which only appear later, marks this anastomosis of two vegetative cells as a sexual process, pseudogamy is often distinguished with difficulty from the usual pseudosexual anastomoses which are brought about by food relations. Its true character is only recognizable cytologically in the pairing of nuclei. If pseudogamy takes place between two sprout cells (Fig. 301, 10 and 11), they are called gametes; in order to avoid misunderstanding, this term should be reserved for merogamous gametes. The ambiguous term **pedogamy,** often used in other senses, may be used to indicate the pseudogamy between adult and young cells (Fig. 93, 17 to 23). The special case of pseudogamy between mother and daughter cell is called **adelphogamy.**

Apomixis, the entire loss of fertilization, represents the last step in this series of reduction of natural sexuality in which growth from reproductive cells takes place vegetatively without cell or nuclear fusion or any external stimulus of development. If the new individuals (in the absence of fertilization) arise from haploid sexual cells, the process is called **parthenogenesis;** if they arise (in the absence of meiosis) from diploid sex cells, the process is called **apogamy.**

For a better summary the different forms of fertilization are tabulated, as far as they concern fungi, according to the scheme of Hartmann:

1. Amphimixis, the copulation of two sexual cells not closely related.
   - *A.* Merogamy. Specific gametes which have arisen as daughter cells of gametangia and serve as sexual cells (*e.g.*, *Synchytrium*, Fig. 11).
   - *B.* Gametangial copulation. Where the differentiation of gametes is suppressed (*e.g.*, *Phytophthora*, Fig. 51).
   - *C.* Hologamy. A special case of gametangial copulation, in holocarpic forms where the whole thallus is transformed into a gametangium and copulation takes place between two mature individuals (*e.g.*, *Polyphagus*, Fig. 26).
2. Automixis. Self-fertilization following copulation of two closely related sexual cells or sexual nuclei.
   - *A.* Parthenogamy. Copulation between two cells of the female sexual organ (*e.g.*, *Ascobolus citrinus*, Fig. 227).
   - *B.* Autogamy. Fusion of nuclei in pairs within a single cell of the female sexual organ, not accompanied by cell fusion (*e.g.*, *Humaria granulata*, Fig. 229).
3. Pseudomixis. Copulation between two vegetative cells.
   - *A.* Pseudogamy. Between cells not closely related to each other (*e.g.*, *Peniophora Sambuci*, Fig. 266, 1).
   - *B.* Pedogamy. Pseudomictic copulation between mature and immature cells (*e.g.*, various yeasts).
   - *C.* Adelphogamy. Pseudomictic copulation of mother and daughter cells (*e.g.*, *Zygosaccharomyces Chevalieri*, Fig. 93, 17 to 23).
4. Apomixis. Vegetative development of sexual cells in the absence of copulation.
   - *A.* Parthenogenesis. Apomictic development of haploid cells.
   - *B.* Apogamy. Apomictic development of diploid cells.

Besides the complication that the original processes of fertilization are replaced in the course of development by all sorts of substitutes, in the study of fungi there is another difficulty. The diagram of a life cycle, (p. 1) which at the instant of fertilization shows a complete transition from the haploid to the diploid phase, describes only the exceptional case in fungi. In the lower fungi, there is simple fertilization where a fusion of two sexual cells (plasmogamy) is followed normally and directly by a fusion of both haploid nuclei into a diploid zygote nucleus, a **syncaryon** (caryogamy); in most fungi, however, caryogamy is delayed and is only completed when the necessity for meiosis appears. Thus the sexual nuclei unite only to form a **dicaryon** in which the paired nuclei pass through their further development synchronously (conjugately); and in this condition possess the same ability to activate the somatic development as after complete caryogamy, although the nuclei remain spatially separate. Their relation corresponds to that of *Cyclops* in which the parent chromosomes remain separate up to the time of egg formation (synapsis!). But in the case of *Cyclops* they are surrounded by the same

nuclear membrane, while in the fungi they remain in their original nuclear membranes.

With this retardation of caryogamy, there goes a spatial separation. The binucleate zygote continues its growth without completing the fusion of nuclei and develops, in the higher fungi, to a new thallus whose cells, virtually diploid, morphologically contain two sexually differentiated haploid nuclei. This new phase, intruded between plasmogamy and caryogamy, is called the **binucleate** phase. To distinguish it from the usual diploid phase we will underline it in the life-cycle diagrams with two thin instead of one heavy line.

It is significant that in spite of this removal and retardation, caryogamy must take place in definite organs. The organs in which the fertilization processes are completed and the dicaryon ends are called **zeugites.** As caryogamy is delayed until the necessity for meiosis appears, these zeugites function in most forms as gonotoconts. The diagram on page 1 might therefore be modified as follows:

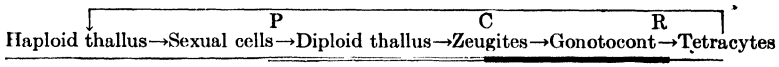


DIAGRAM II.

The two moments, the transformation of the cells which complete the sexual act and the division of the sexual act itself into plasmogamy and caryogamy, separated in time and space, so that reproduction is separated in time and space from the sexual act which brings it about, are both fundamental processes which, since the contributions of Bary and Brefeld, have made possible a deeper interpretation of the classification of fungi created by these two investigators. We shall give special attention to these processes in the rest of the book.

Classification.—Fungi are considered as thallophytes without chlorophyll. In this book, the bacteria and Myxomycetes are not considered. From these two latter classes, the fungi in the narrower sense are distinguished by their diversity of fructifications, from the bacteria by the possession of true nuclei and from the Myxomycetes, excluding groups here considered under the Archimycetes, by the possession of cell walls at all stages of development. In contrast to the Myxomycetes, the other fungi are often called Eumycetes; in other terminology, however, this name is reserved for the Ascomycetes and Basidiomycetes, to distinguish these two classes from the Phycomycetes.

The classification of fungi rests upon the consideration of the life cycle and the development which their thalli and organs of fructification have attained in both portions of the life cycle. On this basis they may be divided into four classes: Archimycetes, Phycomycetes, Ascomycetes and Basidiomycetes. The Archimycetes and Phycomycetes are distinguished by the primitive character of the thallus, naked in the Archimycetes, or

surrounded by a cell wall in the Phycomycetes, and by the limitation of the diplonts to the zygote, in whose germination meiosis occurs; thus the zygote is also gonotocont. The Ascomycetes are distinguished by the more highly developed thallus and, in typical forms, by the development of the zygote to a typical mycelium with meiosis shifted to special reproductive organs; in the Ascomycetes into "sporangia" with free cell formation, the asci; in the Basidiomycetes into "conidiophores" with exogenous abscission of spores, the basidia.

Possibly in time it will be desirable to place at the beginning still a fifth class, the Myxomycetes, as these may be basically separated from the Archimycetes.

CHAPTER V

CLASS ARCHIMYCETES

According to a proposal in a letter from E. Fischer, the fungi here called Archimycetes are the earlier Myxochytridiales. They include naked, often amoeboid forms which develop holocarpic reproductive organs by division of the whole thallus. They stand very close to the Myxomycetes and flagellates and chiefly differ from them in their parasitism.

They are divided into four families: the Olpidiaceae and Synchytriaceae, whose zoospores are oval or pyriform with trailing flagella; the Plasmodiophoraceae, whose zoospores are amoeboid, with an apical flagellum; and the Woroninaceae whose zoospores are reniform with two lateral flagella. The thallus forms a single sporangium in the Olpidiaceae, a sporangiosorus in the Synchytriaceae and a multitude of spores or spore balls in the Plasmodiophoraceae.

At present the relationships of these four families are still obscure. The Plasmodiophoraceae and Woroninaceae, are peculiar on account of their schizogonia; it is questionable, however, whether the formation of sori in the Synchytriaceae may not be an extreme reduction of schizogonia, if the nuclear divisions up to the formation of the protospores and their analogues are called the vegetative phase and the subsequent ones, which lead to zoospore formation, the reproductive phase. Previous studies, however, have given no basis for such considerations. Further, the zoospores of the Olpidiaceae and Woroninaceae, like the swarm spores of many Monadineae, before germination on the host are always surrounded by a membrane, and discharge their contents into the host cell leaving their empty membrane on its surface. The zoospore of the Synchytriaceae and possibly of the Plasmodiophoraceae withdraws its flagellum and then as a whole penetrates the host plant. How far this lack of a membrane may be evaluated phylogenetically is not yet clear.

These four families are regarded as four different lines which have developed independently of each other from the Sporozoa–Flagellate–Myxomycete line. Since in the Woroninaceae and Plasmodiophoraceae, the distinguishing points have not yet been determined cytologically, a discussion of these relationships would be premature.

Olpidiaceae.—This family is very simply organized and, as far as known, reproduction proceeds isogamously by aplanogametes.

In *Olpidium Viciae*, which in spring and early summer causes a disease of *Vicia unijuga* in Japan (Kusano, 1912), the uniflagellate zoospore swims about on the leaves of the host for as long as 24 hours, with short rest periods during which it may creep over the substrate in an amoeboid manner (Fig. 9, 1). When it finally comes to rest it withdraws its flagellum, surrounds itself with a membrane, bores through the wall and discharges its thick naked protoplasm into an epidermal cell of the host, where it attaches itself to the nucleus as an amoeboid protoplast (Fig. 9, 2 to 6). A period of promitotic (or amitotic?), later of mitotic, nuclear division follows, during which the protoplast is surrounded by a membrane and develops to a sporangium. At maturity

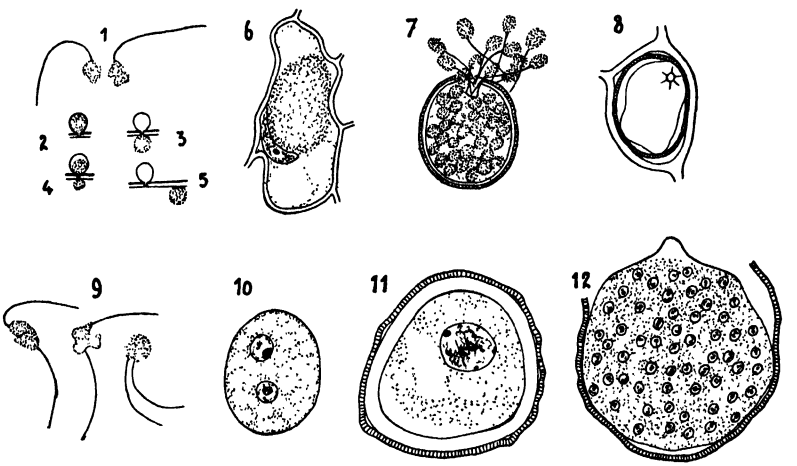


FIG. 9.—*Olpidium Viciae*. 1. Zoospores. 2 to 5. Shedding of membranes and penetration of host cell. 6. Naked thallus of fungus in host cell. 7. Germinating zoosporangium. 8. Empty zoosporangium. 9. Copulation of two planogametes. 10. Young zygote before caryogamy. 11. Mature hypnospore. 12. Multinucleate hypnospore at the beginning of germination. (1 to 9 × 535; 10 × 600; 11, 12 × 1,200; *after Kusano*, 1912.)

(after 5 to 10 days) this pierces the wall of the host cell by rostrate processes and through one of these discharges the zoospores (Fig. 9, 7 and 8).

Under certain conditions, the zoospores behave as planogametes, especially in very ripe sporangia which have consumed the nutriment of the host cell and, while waiting for favorable conditions of nutrition, are passing through a period of hunger. Then they copulate in pairs during pauses in their amoeboid activity. The biflagellate zygote swims about (also with rest periods) and finally comes to rest, surrounds itself with a membrane and discharges its content into a host cell. A definite point of fusion is not present as in the planogametes of the Chlorophyceae;

apparently the plasma membrane may be ruptured at any point. A sexual differentiation is also lacking, indeed two gametes, after attempting to copulate for a few minutes, may again separate. This inner differentiation rests rather on differences in age or turgor.

The young diploid protoplast is binucleate (Fig. 9, 10). When it is mature it is surrounded by a membrane which in time differentiates into an exospore and endospore. Thereby the zygote has become a hypnospore. A fusion of both nuclei occurs in the following spring a few days before germination (Fig. 9, 11). This is followed by numerous mitotic divisions, of which the first is possibly a meiosis. The outer layer of the endospore swells, whereupon the inner layer of the endospore forms an emission collar through the wall of the host cell (Fig. 9, 12) and discharges the zoospore.

Thus the life cycle corresponds to the following scheme (Goeldi and Fischer, 1916):

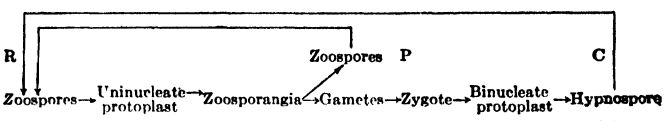


DIAGRAM III.

Haplont and diplont are motile in their young stages and independent in their life functions; accordingly they are true gametophytes and sporophytes. The former, which lacks the diplont may increase repeatedly by zoospores, while the specific duty of the latter is the formation of hypnospores.

A similar life cycle is probably possessed by the numerous other equally parasitic species of *Olpidium*, as *O. Brassicae*, a destructive parasite of seedlings of cabbage, possibly also of lettuce and tobacco. The young protoplasts are uninucleate. Under favorable conditions they may be naked, even in the stage with 32 nuclei. Then they are surrounded by a membrane and on the proximal side develop an emission collar which germinates at the tip (Němec, 1912). The source and germination of hypnospores (Fig. 10, 2) is unknown. In youth, however, they are binucleate, suggesting a previous plasmogamy (Němec, 1922). Similar observations have been made on *O. Salicorniae* on the roots of *Salicornia herbacea* (Němec, 1911).

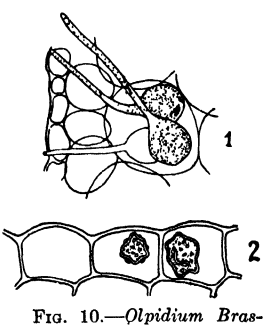


FIG. 10.—*Olpidium Brassicae*. 1. Germinating zoosporangia. 2. Hypnospores within epidermal cells. (× 110; *after Woronin*, 1878.)

Similar to *Olpidium*, but lacking an emission collar, is *Olpidiaster radicis* (*Asterocystis radicis*) parasitic on the secondary roots of many

phanerogams and causing the wilt of flax seedlings in Flanders. Its zygotes are also binucleate in the young stages (Němec, 1922).

Reesia amoeboides on *Lemna* sp. in Germany has the same life cycle as *Olpidium*. It is the first form in which copulation of planogametes was observed by Fisch (1884), but until the work of Kusano, his work was considered erroneous. *Monochytrium Stevensianum* (Griggs, 1910) on *Ambrosia artemisifolia* in the United States appears to be similar, but its life cycle is incompletely known. Also noteworthy is the partially known *Pleolpidium* which parasitizes fungal hyphae, such as *P. irregulare* on *Pythium*. In some respects it reminds one of the Woroninaceae but differs from them in the uniflagellate zoospores. Dangeard (1889, 1895*a*) made similar observations for *Sphaerita*.

Synchytriaceae.—In contrast to the Olpidiaceae, the thallus of this family does not change to a sporangium but to a sporangial sorus partially protruding from the original sheath. Further, their thalli remain uninucleate until the beginning of fructification so that the nucleus may attain a diameter of 25μ.

Synchytrium, chiefly parasitic on phanerogams, is divided into three subgenera according to the method of spore formation: *Pycnochytrium* where the summer spores (if they are produced) are as thick walled as hypnospores and germinate with a protruding sorus; *Mesochytrium* whose summer sori are thin walled but germinate as in *Pycnochytrium;* and *Eusynchytrium* which agrees morphologically with *Mesochytrium*, but forms zoospores inside the membrane of the initial cell. How far these differences are fundamental is still obscure; the protrusion of the sorus may be only the result of a brittleness of the exospore which cannot expand as rapidly as the sorus. In the subgenera *Eusynchytrium* and *Mesochytrium*, the protoplast is yellow or reddish yellow; in *Pycnochytrium*, it varies according to the species and age, from reddish yellow to yellow or hyaline.

In the subgenus *Pycnochytrium*, *S. endobioticum* causes the potato wart on *Solanum tuberosum*, also attacking *S. nigrum* and *S. Dulcamara* (Curtis, 1921). The zoospore swarms especially between 12 and 19°. After it comes to rest on the epidermis of the host, it withdraws its flagellum, throws it off and penetrates the host cell where its body is carried to the bottom of the cell by the streaming of protoplasm (Fig. 11, 1 to 4). The host cell swells under the influence of the parasite and becomes pyriform; repeated division of the neighboring tissue cells forms a tumor; the surrounding epidermal cells divide similarly and become woody so that a rosette is formed with the infected cell in the middle (Fig. 11, 5 and 6).

The zoospore develops to a summer spore, also called prosorus or initial cell, and surrounds itself with a double wall, a thick golden-yellow exospore and a thin hyaline endospore (Fig. 11, 7). Its nucleus reaches

a diameter of 25μ. It completes its maturation by a triple expulsion of chromatin from the nucleolus into the nuclear vacuole. During, or shortly after, the third expulsion, the endospore pushes out a short pro-

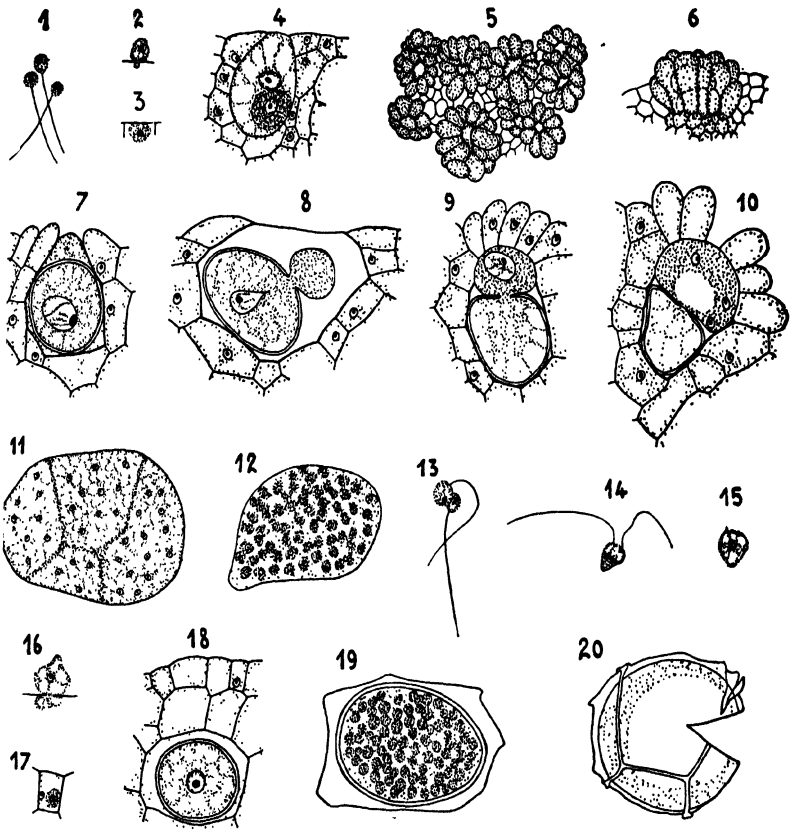


FIG. 11.—*Synchytrium endobioticum*. 1. Zoospores. 2, 3. Penetration of host cells. 4. Young protoplast within a hypertrophied epidermal cell. 5. Group of immature summer spores; the single thickened cells within the rosettes are the infected epidermal cells. 6. Rosette. 7. Mature summer spore. 8 to 10. Germination of mature summer spores. 11. Young sorus, the future walls indicated by the denser protoplasm. 12. Mature zoosporangium with the fundament of the emission collar. 13 to 15. Copulation of two planogametes. 16, 17. Penetration of the zygote. 18. Young hypnospore. 19. Hypnospore during maturation of the zoospore primordium. 20. Empty hypnospore. (1, 12, 19, 20 × 520; 2, 3, 14 to 16 × 1,270; 4, 7 to 10, 17, 18 × 270; 5 × 100; 6 × 115; 11 × 535; 13 × 1,110; *after Curtis*, 1921.)

jection and in about 4 hours the whole content slips into the remaining space of the dead host cell (Fig. 11, 8 to 10). When the number of nuclei reaches the neighborhood of 32 by repeated mitotic division, the protoplasm collects to denser zones (Fig. 11, 11), regardless of the position of

the nuclei, so that the prosorus is divided into 5 to 7, seldom into 9 portions. These portions are surrounded by hyaline membranes; they are the future zoosporangia in which, by further divisions, the number of nuclei increases to as many as 300 (Fig. 11, 12).

At germination the rosette, along with the whole sorus, is pressed to the upper surface by the swelling of the tumor cells; similarly, by pressure on all sides, the sporangia are forced out of the sorus and the disorganised host cell, into the open (Fig. 11, 13) and liberate their numerous zoospores through a narrow slit.

Zoospores from over-ripe sporangia behave as planogametes. A zoospore swims to another which has come to rest and fuses with it (Fig. 11, 13 to 15). It is improbable that zoospores from the same sporangium copulate, although zoospores from different sporangia of the same sorus may.

The zygote, like a zoospore, penetrates the epidermal cell of the host (Fig. 11, 16 and 17); under its influence the latter divides repeatedly so that daughter cells and parasite are pushed several layers of cells deep into the host tissue (Fig. 11, 18).

While the haploid zoospores cause only a hypertrophy of the host cell and the sori arising from them cause a hyperplasia of the neighboring epidermal cells, the diploid zygote or young hypnospore causes hyperplasia of the host so that the resting spore is pushed deeper into the host tissue, but the neighboring epidermal cells remain undivided. Here is an example of the different specific effect of the haplont and diplont on the host, such as we shall find in the Uredinales.

The diploid nucleus extrudes chromatin at least thrice; a true meiosis has not yet been reported. The young hypnospore surrounds itself with a double wall; a third layer is laid down by the protoplasm of the host cell. After a long resting period, usually the next spring, numerous zoospores are formed by repeated nuclear division (Fig. 11, 19); because of the swelling of the innermost wall layer, the hypnospore bursts open and the zoospores are set free in their sorus (Fig. 11, 20).

Closely related to this form is *S. aureum* which lives on more than 100 host plants in very diverse families (Rytz, 1907). A much-enlarged epidermal cell serves as host cell for the fungus. The neighboring cells, especially the epidermal cells, enlarge and occasionally divide to produce a hemispherical growth which often raises the host cell above the plane of the epidermis. The top of the host cell (*i.e.*, the top of the wart) lies in a slight depression. According to observations in the natural habitats, the several strains of fungi formed because of different conditions of living and plant associations, differ on principal and auxiliary hosts, for the principal host may be comparatively regularly infected and the auxiliary hosts under definite, but still unknown conditions. Thus for the *Lysimachia* group (*S. aureum*), the chief host is *Lysimachia nummularia;*

the auxiliary hosts are from *Potentilla, Valeriana, Hypericum, Epilobium* and *Myosotis;* or in the alpine saxifrage groups (*S. Saxifragae*) the principal host is *S. aizoides*, the auxiliary hosts *S. stellaris, S. moschata, Androsace chamaejasme, Hutchinsia, Leontodon, Viola, Ranunculus, etc.*

In *Synchytrium Succisae*, on *Succisa pratensis*, there is a division of labor between the summer sori and the resting spores; the summer sori remain thin walled and only the somewhat smaller hypnospores, in which the fungus winters over, possess a thick double-layered sheath (Rytz, 1907).

In *Synchytrium* (*Eusynchytrium*) *Taraxaci* on *Taraxacum* sp. (Schroeter, 1875; Lüdi, 1901), *S.* (*Eusynchytrium*) *decipiens* on tropical and temperate phanerogams (Tobler-Wolff, 1912) and *S.* (*Eusynchytrium*) *Puerariae* on *Pueraria Thunbergiana* in Japan (Kusano, 1907, 1908), the stage of the projecting blister is omitted; their zoospores arise in the

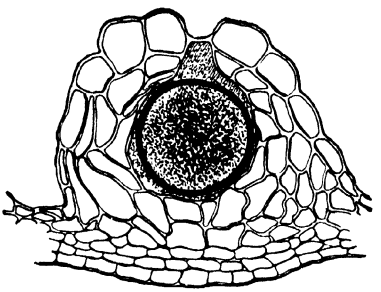


FIG. 12.—*Synchytrium aureum*. Hypnospore in an enlarged epidermal cell, surrounded by a small gall. (× 93; *after Rytz*, 1907.)

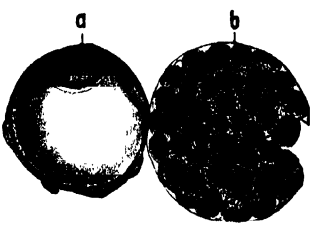


FIG. 13.—*Synchytrium Saxifragae*. Hypnospore, *a*; with sorus, *b*, which has already formed zoosporangia. (× 340; *after Rytz*, 1907.)

initial cells themselves and swarm out of them through an opening. In *S. decipiens*, cleavage of the protoplasm produces uninucleate portions which form the young naked sporangia. They are called **protospores** (Harper, 1899). Their nuclei divide repeatedly so that every sporangium contains several nuclei. In this species, four chromosomes have been counted (F. L. and A. C. Stevens, 1903; Griggs, 1909). In *S. Taraxaci* the protospore stage is omitted and the multinucleate protoplasm, as in *S. endobioticum*, is divided directly into multinucleate sporangia whose nuclear number further increases by division (Dangeard, 1891; Harper, 1899); this division takes place by cleavage from the periphery inwards, not by successive formation of membranes as in *S. endobioticum*.

A fourth subgenus *Woroninella* is distinguished by the crateriform or aecidial habit of its open sori. So far only thin-walled summer spores, germinating as in the *Eusynchytrium* type, are known. *Synchytrium Psophocarpi* in tropical Asia is parasitic on *Psophocarpus tetragonolobus*, *S. vulcanicum* on *Lespedeza cytisoides*, *S. aequatoriense* in Ecuador on

Psoralea Mutisii and *S. aecidioides* (*Uredo aecidioides*) on *Amphicarpa* in the United States (Gäumann, 1927).

Still insufficiently known and hence of uncertain position are *Micromyces* (Dangeard, 1889) in *Zygotonium* in western France, *Sorolpidium* (Němec, 1911, Guyot, 1927) in the cortical cells of *Beta vulgaris* (*B. maritima*) in Czechoslovakia and *Anisomyxa* (Němec, 1913) in the cortical cells of roots of *Plantago lanceolata* in Czechoslovakia. All three agree in that their thalli break up into zoosporangial sori and that the zoospores are uniflagellate. The two latter appear to differ from *Synchytrium* in nuclear relationships.

Plasmodiophoraceae.—In spite of many studies, there is still much doubt in the decisive points of the life cycle, particularly in regard to the peculiarities of nuclear division and the existence of caryogamy. Usually single organs of phanerogams are stimulated to form tumors within which spores are produced.

At spore germination, which generally occurs in spring, there arises from each spore an amoeboid zoospore (myxamoeba) with an apical flagellum, which in *Spongospora* combines with the myxamoebae from other spores (Kunkel, 1915) and penetrates the host. In the first stages of the disease, one finds in the protoplasm of the host cell, one or more naked bodies of protoplasm (myxamoebae) which have penetrated (Fig. 14, 2). They grow markedly and by repeated promitotic nuclear division become multinucleate (schizont stage) and successively cut off daughter amoebae (meronts) as short blunt processes (Fig. 14, 3). With the divisions of the host cells, where such occur, the amoebae are again divided among the daughter cells; however they are also able to wander independently from cell to cell (Kunkel, 1918). The host cells gradually swell up and the schizogonia of the amoebae proceed until the exhaustion of the reserve stores.

Then the amoebae of each host cell join to form a plasmodium, and their nuclei extrude a part of their chromatin (Fig. 14, 4 and 5). Their further phases are still insufficiently known. Prowazek (1905) for *Plasmodiophora Brassicae*, the cause of clubroot of cabbage, and Osborn (1911) for *Spongospora subterranea*, the cause of powdery scab of potatoes, have claimed that some nuclei come together in pairs and fuse, while the surplus nuclei degenerate and disappear; these statements, however, have not been confirmed. In any case there follows a generative period in which throughout the plasmodia, there occur two synchronous, nuclear divisions, one of which is meiotic (Fig. 14, 7); the plasmodia divide into uninucleate portions, surround themselves with a membrane and develop as spores (Fig. 14, 1, 8).

These spores are generally comparatively thick walled and very resistant to external influences. In *Plasmodiophora* (Woronin, 1878; Nawaschin, 1899; Prowazek, 1902, 1905; Maire and Tison, 1909; Favorski,

1910; Lutman, 1913) they lie singly within the host cell and are liberated on its decay; in *Sorosphaera* (Schwartz, 1910, 1911; Maire and Tison, 1909; Blomfield and Schwartz, 1910; Winge, 1913) they are arranged in hollow spheres; in *Sorodiscus* (Winge, 1913) they form ellipsoids; in *Tetramyxa* (Maire and Tison, 1911) they lie in tetrads; in *Spongospora* (Osborn, 1911; Kunkel, 1915) they are joined in spongy masses and in *Ligniera* (Maire, 1911; Schwartz, 1914; Fron and Gaillat, 1925; Cook,

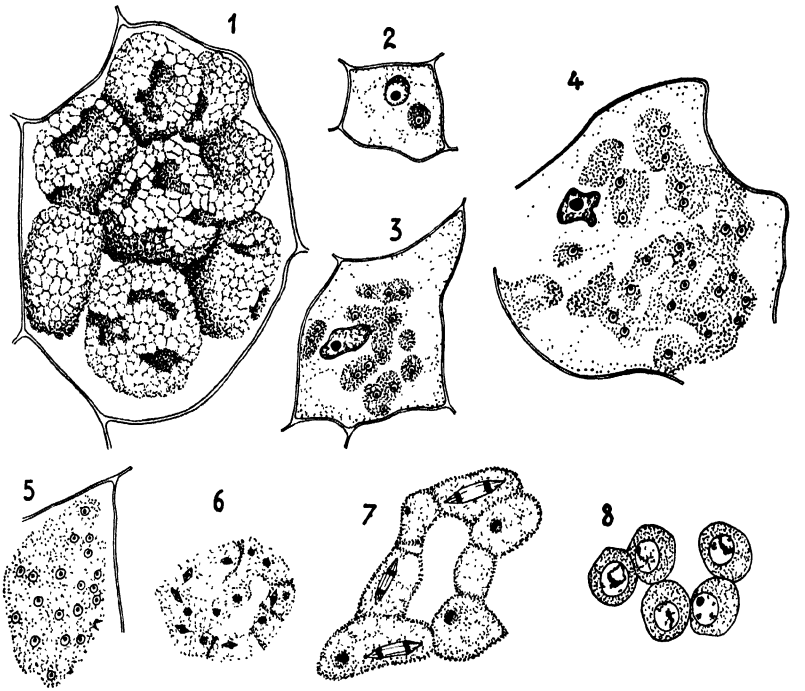


FIG. 14.—*Spongospora subterranea*. 1. Host cell with 8 spore balls. 2. Young amoeba in host cell. 3. Amoebae. 4, 5. Plasmodium formation. 6. Beginning of segmentation of the protoplasm. 7. Beginning spore formation. 8. Mature spores. (1 × 700; 2 to 6 × 600; 7, 8 × 1,830; *after Osborn*, 1911.)

1926, Guyot, 1927) in regular clumps. The last genus does not cause the development of tumors by the host, while all the others cause conspicuous hypertrophies. Only *Plasmodiophora* and *Spongospora* cause disease of economic importance.

An interpretation of the life cycle of the Plasmodiophroaceae is not yet possible. Except for the unconfirmed work of Prowazek and of Osborn, the location of caryogamy is unknown. Similarly the relation of the sporonts to plasmodia needs more careful investigation. Because of this obscurity, a discussion of the relationships of the Plasmodiophor-

aceae to the Myxomycetes and flagellates would be premature; probably they have arisen from these groups and have been much modified by their parasitism.

Woroninaceae.—Since the position of this family is obscure, its classification here is provisional. It contains all biflagellate Archimycetes. The assignment of definite phylogenetic lines is postponed until a greater number of species is known. A representative of each of the more carefully investigated genera will be described.

The zoospores of *Olpidiopsis Saprolegniae* on *Saprolegnia* are ovoid or reniform. The two flagella arise laterally somewhat toward the apex.

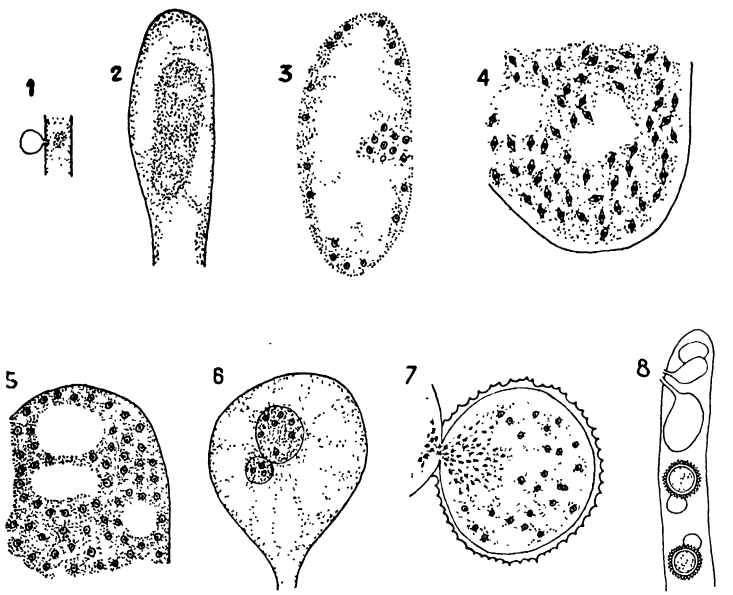


FIG. 15.—*Olpidiopsis Saprolegniae*. 1. The zoospore has formed a membrane and allowed its content to slip into a hypha of the host. 2 to 5. Development of the young protoplast to a zoosporangium. 6, 7. Development of the zygote. 8. Host hypha with 3 empty zoosporangia and 2 hypnospores. (1, 8 × 1,000; 2 × 890; 3, 6, 7 × 670; 4, 5 × 1,370; *after Barrett*, 1912.)

A few minutes after swarming they come to complete rest and after a short rest period, swim on. If they reach a filament of *Saprolegnia*, they show some amoeboid movement, and surround themselves with a wall, while the germ tube pierces the wall of the host hypha, into which the uninucleate cell content is ejected (Fig. 15, 1). By streaming, the naked protoplasm may be carried for a distance in the hypha; it grows rapidly, becomes multinucleate, and after two or three days surrounds itself with a wall and becomes a zoosporangium. At maturity several small vacuoles form and these then flow together into a large central vacuole

(Fig. 15, 3), push toward the periphery and, after completing a nuclear division, cut up the protoplasm next the wall into uninucleate zoospore initials. These grow with equal rapidity, fill out the sporangium and thereupon contract, perhaps by the expression of water. Finally they begin to swarm from the emission collar (A. Fischer, 1882; Schwarze, 1922).

The formation of hypnospores in the poorly nourished hyphae is preceded by a sexual act. Around one larger multinucleate protoplast, one or more equally nucleate, smaller male protoplasts are placed (Fig. 15, 6). Each is surrounded by a membrane which in the female cell, except for the point of contact with the male, is thickened and echinulate while the male remains thin and smooth. At fertilization the separating wall dissolves and the whole content of the male cell passes into the female (Fig. 15, 7). If several male cells are present, apparently all can discharge their content into the female.

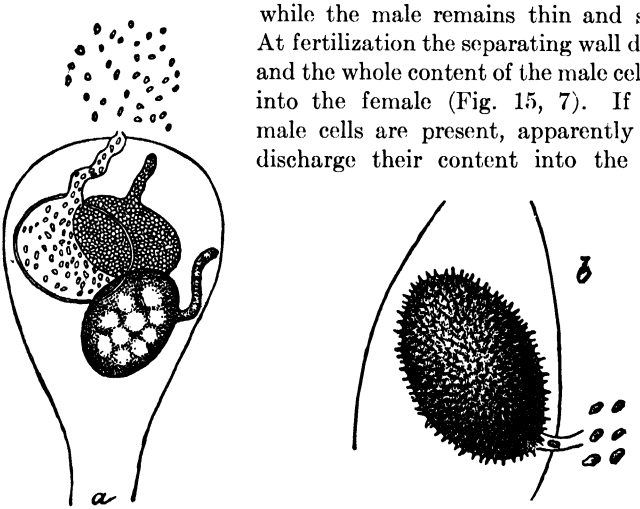


FIG. 16.—*Pseudolpidium Saprolegniae*. *a*, swollen host hyphae with 3 sporangia; *b*, hypnospore. (× 320; *after A. Fischer*, 1882.)

The empty male cell membranes remain connected to the zygote as "appendiculate cells." The further fate of the nuclei is unknown. The endospore becomes brown and thickened while the echinulate exposore remains hyaline. They germinate by zoospores which discharge through an emission collar (Barrett, 1912).

Pseudolpidium Saprolegniae, also parasitic on *Saprolegnia*, in structure and habit resembles *Olpidiopsis* but differs in the absence of "appendiculate cells" on the hypnospores (Fig. 16*b*). An insufficiently known species found by Serbinov (1907) on algae, suggests *Woronina* and *Rozella* in the peculiarity of its young amoeboid protoplasts, which divide by constriction.

The species of *Woronina* are parasitic on algae and fungi. In *W. polycystis*, on *Saprolegnia* (A. Fischer, 1882), the zoospore on the host hyphae

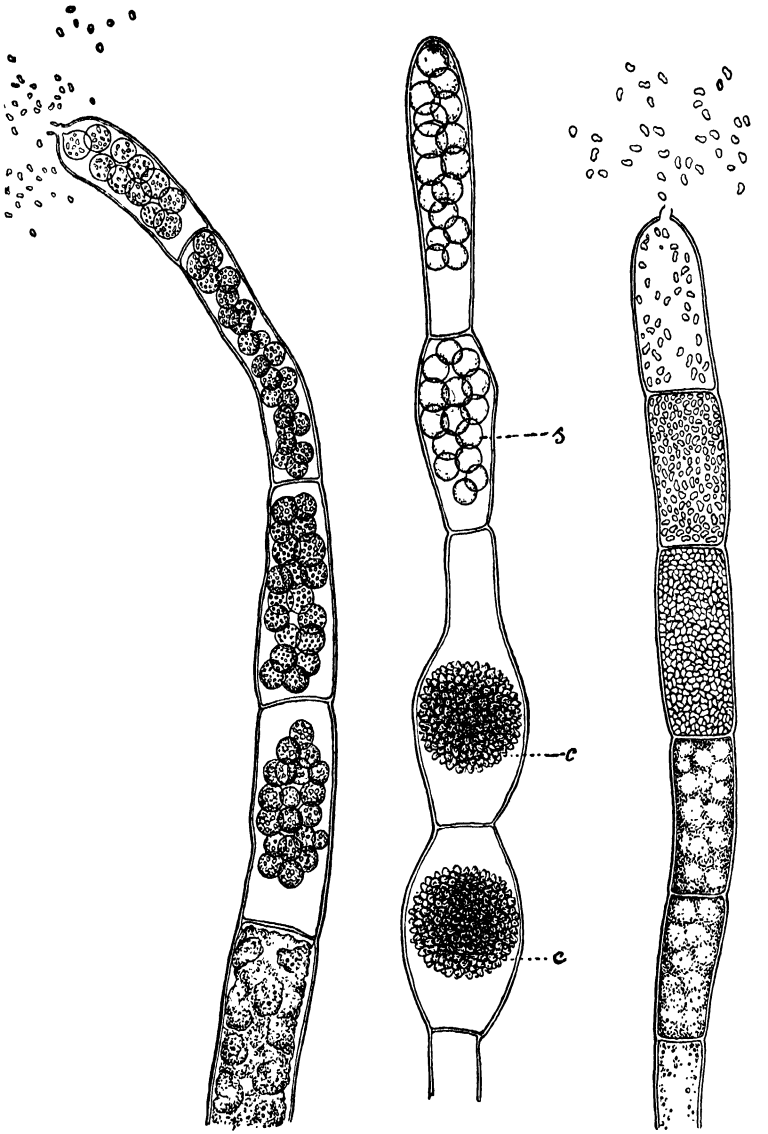


FIG. 17.—*Woronina polycystis*. *a*, Hyphal tip of *Saprolegnia* with 5 cells each containing a sporangial sorus of the parasite, the uppermost about to discharge; *b*, Cystosorus, *c*, in each of lower cells, a sporangiosorus, *s*, in the upper cells. *c*. *Rozella septigena*. Hypha tip of *Saprolegnia* with 5 cells each entirely filled with a cylindrical zoosporangium. (*a* × 200, *b* and *c* × 300; *after Cornu*.)

surrounds itself with a membrane, and discharges the naked protoplast into the interior. This is carried to the tip of the hypha by the streaming protoplasm and there separated from the host by a septum. It grows rapidly at the expense of the host plant and after two days breaks up into polyhedral portions (the young zoosporangia) each of which rounds off and surrounds itself with a membrane. At maturity they form a short papilla which pierces the host wall and allows the zoospores to escape.

With falling temperature in stagnant water, resting conditions appear. The individual sporangia are surrounded by a strong membrane, adapted to resting over unfavorable conditions. A. Fischer calls them **sporangiocysts.** They are joined to a thick group (**cystosorus**) which is derived as a whole from a single protoplast (Fig. 17*b*). At germination the sporangiocysts change into sporangia and, in a still unknown manner, discharge the zoospores into the open.

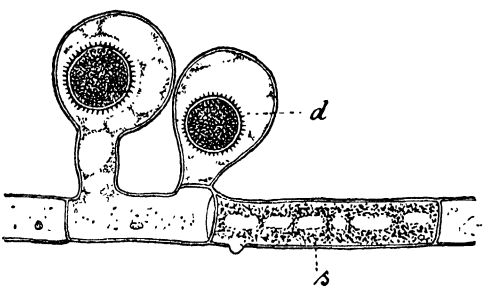


FIG. 18.—*Rozella septigena.* Part of host hypha with the false oogonia, each containing an echinulate hypnospore, *d*, containing the parasite; *s*, sporangium of the parasite. (× 400; *after Cornu.*)

Rozella septigena lives exclusively on *Saprolegnia* hyphae, (A. Fischer, 1882). As in *Woronina polycystis*, the parasite, after penetration, passes with the streaming protoplasm to the apex where it divides repeatedly, so that the daughter individuals are separated occasionally by the septa of the host. Hence they lie behind one another in a row of single flabella (Fig. 17*c*). After approximately two days, each changes to a sporangium whose walls lie directly on that of the host hyphae. Thus a filament infected by *Rozella* has the appearance of a hypha which has cut off several gemmae. At germination the sporangium collects its protoplasm to a thick covering on the walls, and cleaves into single zoospores which swarm out through a papilla. The hypnospores arise in lateral outgrowths of the single flabellum; their wall is closely echinulate (Fig. 18). Their formation and germination are unknown.

Belonging to the Woroninaceae or closely related to them is a series of interesting forms whose life cycles are imperfectly known, as *Pyrrhosorus marinus* (Juel, 1901) and *Pleolpidium inflatum* (Butler, 1907).

CHAPTER VI

CLASS PHYCOMYCETES

The Phycomycetes owe their name to the fact that they were long considered as degenerate algae. Because of their similarity to the Siphonales, they are sometimes called Siphonomycetes.

The thallus, in contrast to that of the Archimycetes, is surrounded by a membrane. In the simpler forms, it is a uninucleate cell; in the higher forms a true mycelium with aseptate multinucleate hyphae; in the highest forms, the hyphae are abjointed into uni- or multinucleate cells. In several families the hyphae may fragment and become a sprout mycelium.

Sporangia and conidia are fructifications of the haplont. In the simplest forms, sporangia arise by a change of the thallus; in the forms with a better developed thallus, they are eucarpic, with special organs which occupy only a part of the thallus. In time, such a small part of the thallus is used for the formation of sporangia that these may be repeatedly formed on nearly all the hyphae of the plant; thus the reproductivity of an individual is increased many times.

At maturity the sporangia are generally coenocytic. By the individualization of single energids, they produce motile zoospores, or by the cleavage of the protoplasm into multinucleate portions, non-motile sporangiospores. By the combined effect of several factors, especially by the transition from submersed to terrestrial and finally to parasitic habits, the development is gradually inhibited before the daughter cells have individualized: the sporangia germinate as a whole with a coenocytic germ tube. Subsequently they assume the task of propagation instead of their daughter cells, and become successively spores and conidia.

By this degeneration of sporangia to conidia, the number of propagative organs formed by an individual is greatly reduced. This numerical disadvantage is offset by a considerable increase of branching of the conidiophores, whereby the number of sporangia formed by an individual increases in geometric progression. *Aplanes Braunii* and *Pythium Indigoferae*, however, are on the point of giving up their degenerate asexual reproduction in favor of the sexual, and in many Entomophthoraceae and Endogonaceae, only the sexual reproduction is known. The preference for sexual reproduction at the cost of the degenerate asexual, will be met later in a greater degree in the Ascomycetes and Basidiomycetes.

As sexual organs, gametangia and gametes are formed. In the lower forms, the gametangia arise like the sporangia by the transformation of

the whole thallus; they are then only sporangia whose zoospores, possibly because of undernourishment, are no longer capable of further independent development. In the higher forms, however, again like sporangia, they arise as special organs, antheridia, oogonia, etc., which finally engage only a small part of the thallus; in many of these forms, however, conditions of nourishment alone determine whether a fundament develops to a sporangium or gametangium. Only in the highest Phycomycetes is the gametangium so highly specialized that it is unable to change into a sporangium, and degenerates in the absence of a mate.

These close relationships between sporangia and gametangia increase, so that in the Phycomycetes, the gametangia undergo changes in the course of their phylogenetic development similar to those in sporangia; just as in sporangia, the individualization of spores is absent and the sporangia assume the task of the spores so in the gametangia, individualization of the gametes is lacking; hence the gametangia remain coenocytic and allow their contents to fuse without differentiation. Gametangial copulation appears between two coenocytic gametangia instead of copulation of gametes. These tendencies appear in the lowest holocarpic families and naturally lead to hologamy; as the differentiation of gametes is absent, the whole thalli fuse and form a single coenocytic zygote. In the higher forms, gametangial copulation, except in *Monoblepharis*, is the only type of sexuality known. The original complexes which lead to suppression of individualization of gametes and copulation of coenocytic gametangia, have not yet reached pure gametangial copulation; their reduced activity in the nuclei leads, in the higher forms, to the appearance of privileged sexual nuclei, appearing in both the isogamous and the heterogamous series.

Corresponding to this variation in development of gametangium and gametes, the zygotes are not entirely equivalent in the Phycomycetes. Externally they appear rather similar, as, almost without exception, biologically they are hypnospores; ontogenetically they may be divided into true zygotes and coenozygotes the product of two coenocytic gametangia. As a conidium corresponds to many zoospores and hence the probability of dispersal is numerically only a fraction of that represented by the totality of these zoospores, a coenozygote corresponds to a large number of true zygotes and has, by analogy, only a fraction of the probability, represented by the totality of true zygotes, to rest over unfavorable times and to reach a favorable substrate. Hence it is significant that in the coenozygotes, the formation of fructifications appears first in the fungi. In the highest Oomycetes, the coenozygotes remain enclosed in the sheath of the female gametangium whose wall undergoes much thickening, and in the higher Zygomycetes they are imbedded in a sheath of closely intertwined hyphae, rich in reserve materials.

Retardation of development, similar to that in the gametangia before the gametes were individualized, may be recognized in the zygotes and coenozygotes; in them caryogamy is first postponed and then shifted in place. These tendencies will be discussed more in detail in the Ascomycetes.

The life cycle of most forms resembles that of the simpler Chlorophyceae: the thallus and the fructification is haploid and the diplont is limited to a zygote at whose germination meiosis probably occurs.

The systematic classification of the Phycomycetes is based on the developmental forms of the haplont and the structure of the sexual cells. Three orders are generally distinguished, the Chytridiales, the Oomycetes and the Zygomycetes. In the Chytridiales, the thallus is unicellular and poorly developed; in the Oomycetes and Zygomycetes it consists of a highly developed, generally ramose, aseptate, coenocytic mycelium. The Oomycetes are heterogamous; the content of their female gametangia changes into one or more egg cells which are fertilized by sperms or undifferentiated sexual cells (oogamy). The Zygomycetes are isogamous; the contents of their gametangia is not further differentiated, but mixes with the content of a second morphologically equivalent gametangium (zygogamy). The Chytridiales and Oomycetes are generally aquatic, the Zygomycetes terrestrial. The question of their origin and mutual relationships will be discussed later under the individual orders

CHAPTER VII

CHYTRIDIALES

In the present work, the Chytridiales, often called Chytridineae, include the Mycochytridineae; they are parasitic or saprophytic, usually in water, rarely on land. In the lowest forms, the thallus consists of one or more spherical cells, parasitic within the host. In the higher forms it is extramatrical and sends pseudopodia-like haustoria into the substrate; in the highest forms it develops a tubular coenocytic mycelium which may be differentiated into a basal part serving for nourishment and an apical portion serving for reproduction.

Zoosporangia and hypnospores are known. The lowest forms are holocarpic; *i.e.*, the whole thallus forms a fructification. The higher forms are eucarpic; *i.e.*, fructifications are formed from only a portion of the thallus. Both the zoosporangia and the hypnospores germinate by zoospores, which are generally uniflagellate, exceptionally aflagellate; their emission takes place through openings in the mother-cell wall or by emission collars. In the individual details of their formation and liberation, particularly in the varied manner of their accumulation at the mouth of the emission collar, important ontogenetic problems are still hidden.

In some species, the formation of hypnospores is preceded by a sexual act, which occurs between two zoospores which behave as planogametes or between two plants or between two daughter cells of the same plant which have been transformed into gametangia.

The systematic position of the Chytridiales has been controversial. By Bary (1884), Brefeld (1889), Zopf (1890) and Petersen (1910), they are regarded as derivatives of the higher Phycomycetes, particularly of the Zygomycetes, which as a result of their parasitic and aquatic habits, have undergone considerable degeneration. By Bessey (1903), they are connected with the Cladophoraceae in which they had degenerated beyond the Valoniaceae and Botrydiaceae. By Fisch (1884), Dangeard (1889), A. Fischer (1892), Serbinov (1907), Atkinson (1909*a*), Cavers (1915) and Scherffel (1925), they are considered as primitive organisms which, because of the regular appearance of flagellate, often amoeboid, zoospores and simple forms of sexuality, may not be explained by degeneration.

While this last conception is becoming generally accepted, it does not suggest where the roots of the Chytridiales may be sought. Fisch (1884),

Lagerheim (1893), Kusano (1912) and Griggs (1912) suggest a derivation from algae, especially the Phyllobieae, by adaptation to parasitism. Lotsy (1907) and Vuillemin (1907) consider the biflagellate forms at least, are derived from the Isokonteae, while the uniflagellate forms were much simpler and not related to the former. Dangeard, A. Fischer, Cavers and Scherffel finally emphasize their relationship with the Protozoa, especially with the Monadineae (Pseudosporeae) *e.g.*, *Aphelidium* and *Aphelidiopsis*. It is possible that the Chytridiales include entirely heterogeneous elements which appear to converge because of the leveling influences of aquatic and parasitic habits.

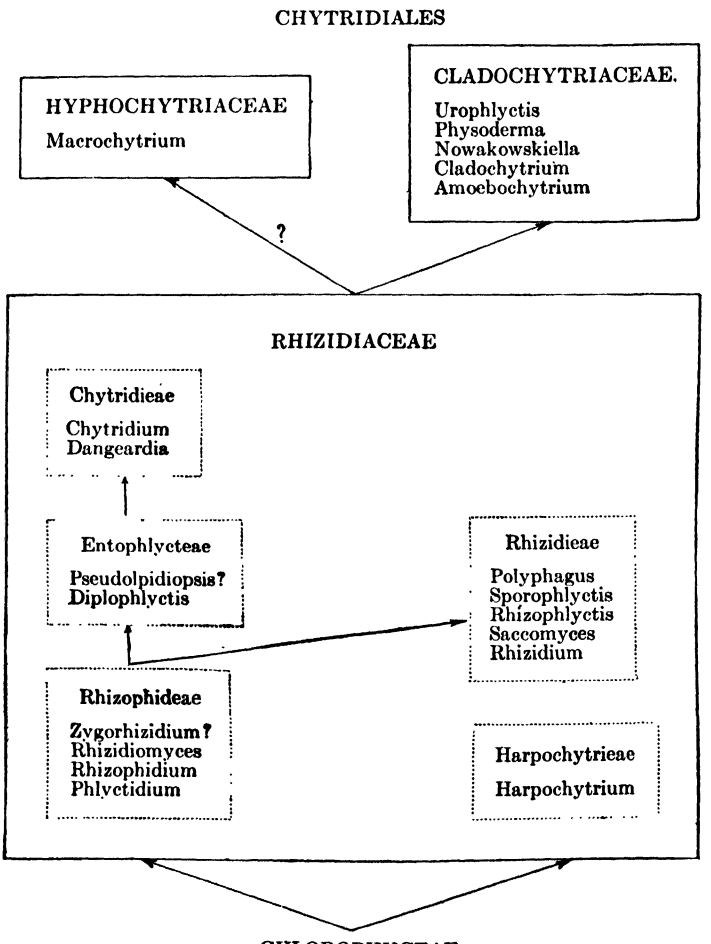


DIAGRAM IV.

The present systematic classification of the Chytridiales is only provisional. At present a large number of very old, slightly related forms are known. As it would be inconvenient to divide them into monotypic families, they have been grouped into larger families but it must be remembered that only a few of them are natural. As only in Central Europe and Eastern United States have they been extensively collected, it is probable that many of the present gaps will be filled.

The above diagram follows essentially that given for the Mycochytridineae (A. Fischer, 1892; Minden, 1915). According to the height of development of the thallus, the Chytridiales are divided into three families; the Rhizidiaceae, Hyphochytriaceae and the Cladochytriaceae. The Rhizidiaceae are holocarpic; their thallus consists of processes (rhizoids) without nuclei and therefore always dependent on the central body which develops into a sporangium. The rhizoids penetrate the substrate like haustoria: they correspond approximately to the pseudopodia of the Rhizopoda. The Hyphochytriaceae and Cladochytriaceae are eucarpic: their thallus is formed as a true mycelium which is divided into principal and secondary axes. The latter possess peculiar swellings with still unknown functions, the turbinate cells.

Whether and how these three families are connected is still obscure. It is possible that the Entophlycteae, Chytrideae and Rhizidieae, may be derived from Rhizophidieae-like forms and perhaps the Cladochytriaceae and Hyphochytriaceae from the Rhizidaceae. Opinion is also divided on their relation to the four families of the Archimycetes; thus Minden (1915) considers it possible that the Rhizidiaceae may be derived from the Olpidiaceae, while Serbinov (1907) considers both families phylogenetically distinct. The Archimycetes seem to be foreign to true fungi and connected with the Myxomycetes and Protozoa. Gäumann would derive the Chytridiales from the Chlorophyceae and consider them as a phylogenetic starting point for the greater part of the fungi.

In spite of these obscurities and in order to give a preliminary exposition of the system of the Chytridiales on page 34, these three families have been juxtaposed on the basis of their morphological similarities. Obviously this scheme in no way corresponds to the natural phylogenetic relationships.

Rhizidiaceae.—This family includes chiefly parasitic forms. There are two distinct lines of development; either a species limits itself to one host individual (monophagy) and by reduction of the extramatrical parts, penetrates far into the host, *i.e.*, passes from ecto- to endoparasitism, or the extramatrical part of the thallus develops as much as possible and infects a large number of hosts (polyphagy) thus increasing the amount of available nourishment. These latter forms are ectoparasitic. Transitional forms are shown between the Rhizophidieae and Entophlycteae, where some forms of the Rhizideae show tendencies to polyphagy.

In order to classify the various genera they have been divided into subfamilies of which five will be discussed here.

The *Rhizophideae* include a series of forms whose sporangia and hypnospores arise directly from the stronger zoospores. After a swarm period zoospores cling fast to the substrate, surround themselves with a membrane and push a process into the substrate and themselves swell to sporangia.

In *Phlyctidium brevipes* on *Spirogyra* in North America this process is still short and scarcely able to penetrate the wall of the host cell. The zoospores disappear through an emission papilla at the top; if after a certain time they have not found a suitable substrate, they may shed their membrane (Atkinson, 1909).

Rhizophidium pollinis (Zopf, 1887) is easily found on *Pinus* pollen in stagnant water (Fig. 19*a*) and oospores of the Peronosporaceae (Melhus, 1914). In the interior of the pollen grain the germ tube branches to a small rhizoid fascicle. The sporangium discharges its zoospores through

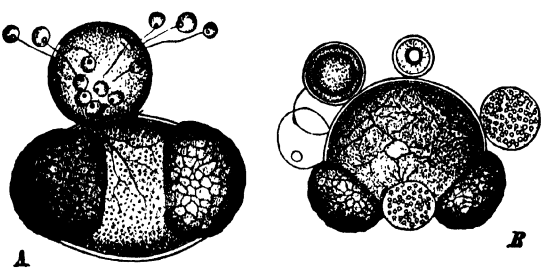


FIG. 19.—*Rhizophidium pollinis*. *A*, zoosporangium on a pollen grain; *B*, Hypnospores and zoosporangia. (*After Zopf*, 1887.)

several sharply limited, punctate germ pores whose membranes dissolve at maturity.

In *Rhizidiomyces apophysatus* (Zopf, 1885), parasitic on the oogonia of many Saprolegniae, the germ tube on the inside of the oogonial wall swells up to an apophysis, out of which the rhizoids pass (Fig. 20, 1). The significance of this subsporangial sac is not yet clear. Directly before zoospore formation, the sporangia form a long emission collar which swells up like a sac at the tip (Fig. 20, 2). Into this sac the zoospore initials pass singly as small bits of protoplasm and are then liberated by the solution of the sac (Fig. 20, 3). Hypnospores are unknown.

Zygorhizidium Willei (Loewenthal, 1905) corresponding in the type of sexuality to the Rhizideae and in the manner of opening its zoosporangia to the Chytrideae, is parasitic on *Cylindrocystis Brebissonii* of the Mesotaeniaceae in Norway. The structure of its thallus corresponds to that of *Rhizidiomyces*, although its zoospores are not liberated by an emission collar but by the dehiscence of a lid (Fig. 21, 5).

The formation of resting spores is preceded by a sexual act by which a small male plant sends out an extramatrical copulation tube to a neighboring, larger, similar female plant into which the nucleus and most of the male cytoplasm migrates (Fig. 21, 6 to 8). The female plant sur-

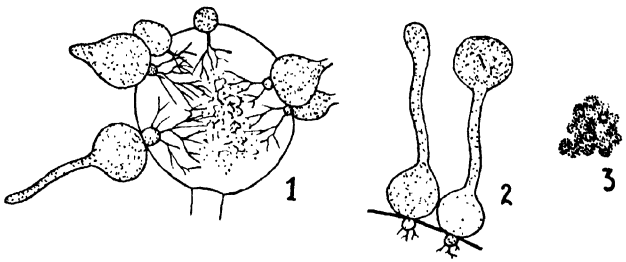


FIG. 20.—*Rhizidiomyces apophysatus*. 1. Oogonium of *Saprolegnia* with sporangia in different stages of development. 2. Beginning germination. 3. Beginning differentiation of zoospores. (× 360; *after Zopf*, 1885.)

rounds itself with a firm membrane and becomes a hypnospore, whose method of germination is unknown.

The Entophlycteae continue the tendency of the Rhizophideae, first formulated by Atkinson (1909*a*), to penetrate deeper into the host cell. In *Diplophlyctis intestina*, a hemiparasite on *Nitella*, the zoospores, after

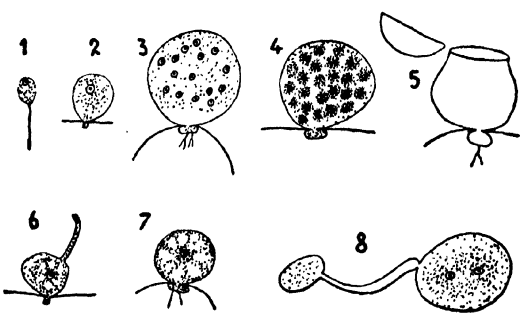


FIG. 21.—*Zygorhizidium Willei*. 1. Zoospore. 2. Young individual. 3 to 5. Evacuation of zoosporangium. 6. Male individual and copulation process. 7. Female individual. 8. Plasmogamy. (× 1,500; *after Löwenthal*, 1905.)

they have been surrounded by a membrane, form a germ tube and an intramatrical sac, called a **germsphere** by Zopf (1885). In contrast to *Rhizidiomyces*, however, the zoospores transfer their whole content into this bladder, whereupon the original zoospore membrane dissolves and disappears (Fig. 22, 1). The germsphere puts out a rhizoid which swells to an apophysis at its point of exit. While the rhizoid elongates and branches, the germsphere swells to a sporangium which at maturity

pierces the host membrane by an emission collar and emits amoeboid zoospores.

In winter this germsphere is transformed as a whole into a thick-walled hypnospore (Fig. 22, 2) which germinates in the spring with zoospores liberated through an emission collar. Thus in *Diplophlyctis*, the whole development is shifted one step further into the host cell than in *Rhizidiomyces*. *Pseudolpidiopsis Schenkiana*, parasitic on Zygnemaceae, is systematically placed differently by various authors. Lotsy (1907) and Minden (1915) have placed it in the Olpidiaceae, although the original author, Zopf (1885, p. 169) expressly stated that in contrast

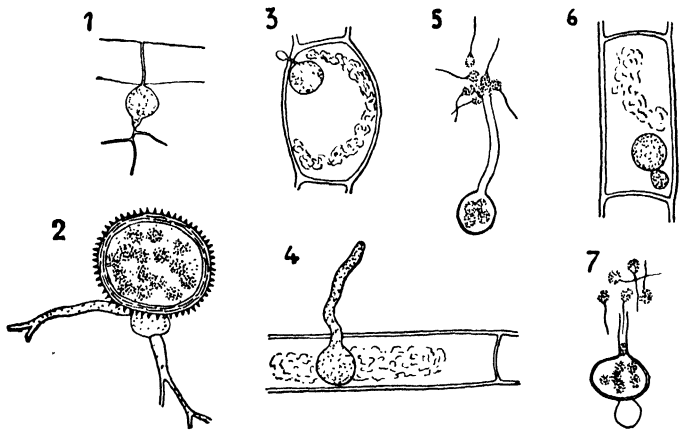


FIG. 22.—*Diplophlyctis intestina*. 1. Fresh point of infection. The zoospore membrane has disappeared by solution. The germ sac has formed a short rhizoid which is about to swell to an apophysis at its point of attachment. 2. Thick-walled hypnospore with apophysis. *Pseudolpidiopsis Schenkiana*. 3. Fresh infection. The zoospore membrane has already gelified and the germ sac is about to swell to form a zoosporangium. 4, 5. Germinating zoosporangia. 6. Copulation of a small male and large female. 7. Germinating hypnospore; the male is still recognizable as an empty sac. (1, 2 × 600; 3 to 7 × 200; *after Zopf*, 1885.)

to the Olpidiaceae, no naked protoplast penetrates the host cell and, therefore, he classed it in the Ancylistaceae. Whether it belongs to the Ancylistaceae or Rhizidiaceae will depend mainly on the number of flagella and type of fertilization. If the zoospores are uniflagellate, as Fisch and Zopf state, they belong to the Rhizidiaceae. If they are biflagellate and if fertilization is oogamous, as Scherffel (1925) states, they belong to the Ancylistaceae. The latter solution is also suggested by its similarity to dwarf specimens of *Myzocytium*.

As soon as the zoospores reach the host, they surround themselves with a membrane and put forth a germ tube which swells to a germ sac within the host cell. This matures to a zoosporangium while the swarm

spore membrane and infection tube degenerate. Zoospores soon develop in the zoosporangia, remain for a short time lying before the opening of the emission collar, there undergo some amoeboid alterations in form and finally swim away (Fig. 22, 4 and 5). In a related species, *P. Oedogoniorum*, the whole content of the zoosporangium may pass out of the emission collar and be differentiated into individual zoospores.

In the sexual plants, the germ sac is divided into a smaller male and a larger female sexual cell (Fig. 22, 6). The content of the male passes over into the female. This as a whole (?) becomes a hypnospore, thickens its wall, so that the male cell, as in *Olpidiopsis*, remains attached as an empty cell. Germination follows by zoospores which escape through the emission collar (Fig. 22, 7).

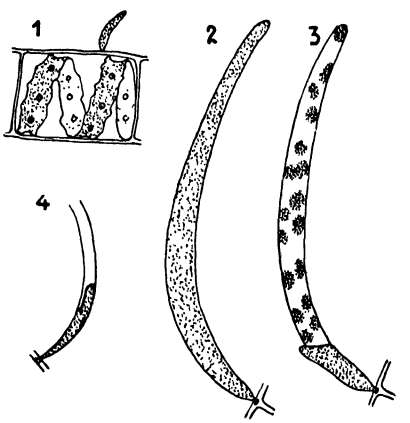


FIG. 23.—*Harpochytrium Hyalothecae*. 1. Young parasite on *Spirogyra* filament. 2. Mature individual. 3. Swarming of zoospores and lateral growth of zoosporangium. 4. Empty zoosporangium showing the beginning of proliferation. (*After Atkinson*, 1903.)

The *Harpochytrieae*, because of their unusual habitat and the peculiar proliferation of the zoosporangia, known elsewhere only in the Cladochytriaceae, are unique in the Chytridiales.

In *Harpochytrium Hyalothecae*, which is parasitic or saprophytic on numerous green algae (Atkinson, 1903; Dangeard, 1903), the germinating zoospore forms a small germ tube which swells to a hapteroid structure between the lamellae of the cell wall of the host or within the cell (Fig. 23, 2). Rhizoids are absent. The young thallus is uninucleate. Nuclear division begins later and the plant divides into a short stipe cell and a long sporangium which discharges the zoospores through an opening at the tip (Fig. 23, 3). After evacuation, the stipe cell grows into the empty sheath of the sporangium, and develops a new sporangium, repeating the process several times. Resting stages are unknown.

Related to it, or perhaps identical with it, is the somewhat larger *H. Hedenii* which is found on Zygnemaceae in North America, Europe, Patagonia and Thibet. This disconnected area suggests great age.

The *Chytridieae* agree in structure and development with the Rhizophidieae, but their resting spores develop intramatrically, as in *Dangeardia mamillata* (Schröder, 1898) on *Pandorina morum* and *Chytridium olla* on oogonia of *Oedogonium*. Their sporangia open by a flat lid covered with blunt spines. The method of formation of hypnospores is unknown; their germination takes place through the formation of a simple tube which ruptures the wall of the host and forms a sessile, covered sporangium.

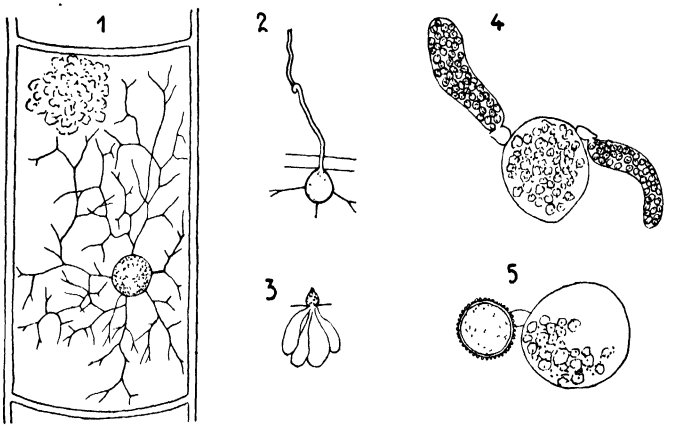


FIG. 24.—*Entophlyctis Cienkowskianum*. 1. Cell of *Cladophora* with a sporangiferous plant. 2. Empty zoosporangium. *Saccomyces Dangeardi*. 3. Four-lobed haustorium. 4. Cell of *Euglena* with germinating zoosporangia. 5. Hypnospore. (1, 2 × 200; 3 to 5 × 280; *after Zopf*, 1885, *and Serbinov*, 1907.)

Of all these tribes, the *Rhizidieae* are the highest in development both in thallus and in sexuality; in the monophagic forms, the zoospores have partially lost their importance as central sacs and are replaced by germ sacs which simultaneously serve as sporangia.

The monophagic forms are closely connected to the Rhizophidieae and Entophlycteae. In *Entophlyctis Cienkowskianum*, parasitic or hemisaprophytic on filaments of *Cladophora*, the zoospores, as in *Diplophlyctis*, put forth a germ tube which swells to a germ sac and takes up all the protoplasm of the zoospores. In exceptional cases, the zoospore sheath may be retained as a knob as is the rule in other species, *e.g.*, *R. bulligerum*. The germ sac develops to a spherical or pyriform sporangium discharging its zoopores through an emission collar which often projects far out into the water (Fig. 24, 2). In some species aplanospores are occasionally formed (Zopf, 1885). At the beginning of the cold season,

the sporangial sac changes into a thick-walled hypnospore whose germination is not yet known.

Because of the type of its germination, *Saccomyces Dangeardii* (Serbinov, 1907), which in Russia is parasitic on resting *Euglena*, is assigned to the polyphagic genera. Its thallus consists of a slightly developed, pyriform, extramatrical portion, a strengthened swarmspore body and a much-branched intramatrical rhizoid tuft (Fig. 24, 3). At the formation of the zoospores, the content of the extramatrical part passes out into a pyriform sac where, inside the membrane, it breaks up into zoospores (Fig. 24, 4), which in turn are freed by degeneration of the sac wall. Hypnospores are formed asexually instead of sporangia.

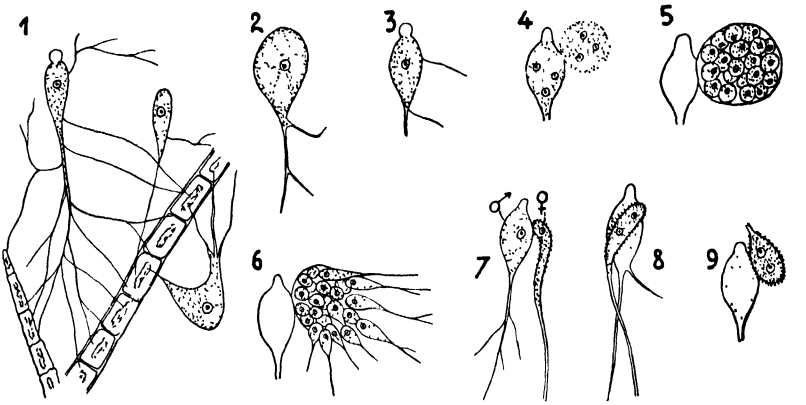


FIG. 25.—*Sporophlyctis rostrata*. 1. Infected filaments of *Draparnaldia glomerata*. 2. Young individual. 3. Mature individual. 4 to 6. Akinete formation. 7 to 9. Copulation. (× 400; *after Serbinov*, 1907.)

In the following species an extramatrical development of the thallus becomes prominent, so that the single individuals simultaneously penetrate several plants of gregarious hosts, as in *Rhizophlyctis Brauniі* which is parasitic or saprophytic on diatoms and desmids.

A similar species is *Sporophlyctis rostrata* (Serbinov, 1907) whose thallus is extramatrical except for the last fine filaments which penetrate the host cell (Fig. 25, 1). The saccate portion of the strengthened zoospore is originally uninucleate, but becomes multinucleate by repeated nuclear divisions. At maturity, the whole content passes out into a sac (Fig. 25, 4) and there breaks up into uninucleate, non-motile akinetes which are liberated by the rupture of the membrane (Fig. 25, 6). Copulation precedes the formation of hypnospores. Two individuals fuse, the content of the male passing over into the female (Fig. 25, 7 to 9). The wall of the hypnospore consists of two layers. Otherwise its development is unknown.

The highest stage of development is reached by *Polyphagus Euglenae*, parasitic on resting stages of *Euglena* (Nowakowski, 1876: Dangeard, 1900; Wager, 1913). Its zoospores are very large, 5 to 13 × 3 to 5μ

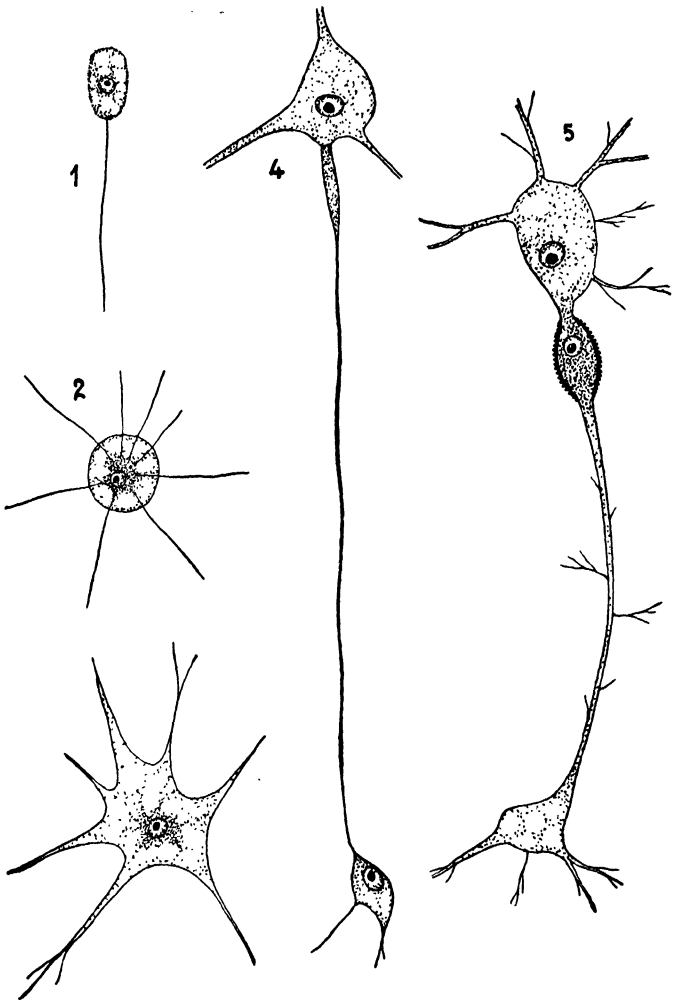


FIG. 26.—*Polyphagus Euglenae*. 1. Swarming zoospores. 2, 3. Thallus with pseudopodia. 4. Beginning copulation. 5. Young zygote, female nucleus about to enter copulation tube. (1 to 3 × 670, 4, 5 × 510; *after Wager*, 1913.)

(Fig. 26, 1). After they have come to rest and surrounded themselves with a membrane, they form the first rhizoids in 1½ to 2 hours. These grow rapidly and in 3 hours become 5 to 6 times the diameter of the

central sac which is the original strengthened zoospore. In this condition, the plant looks like a young heliozoan (Fig. 26, 2). On the other hand, if the zoospore germinates in contact with a *Euglena*, the sac is sessile and the plant looks like a *Rhizidium* or a *Chytridium*. Later the rhizoids branch greatly and can infect as many as 50 Euglenae. The

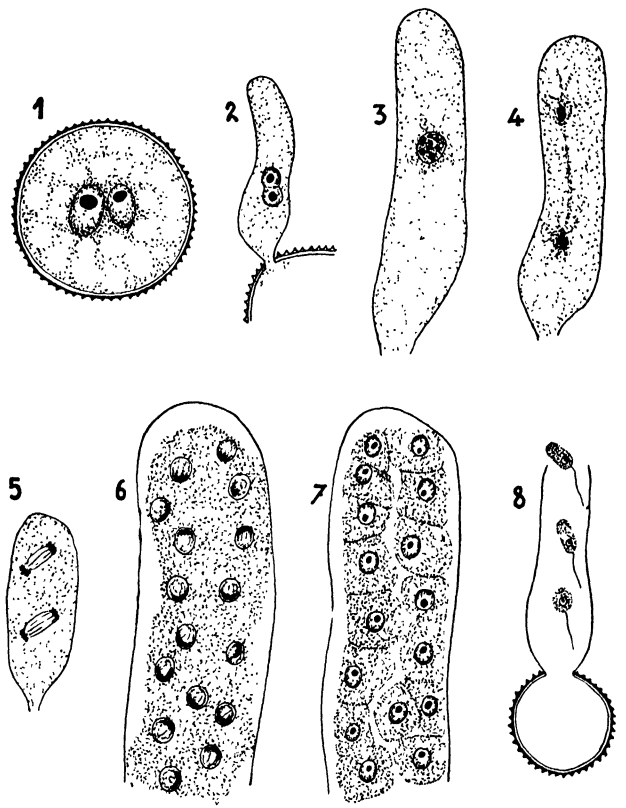


FIG. 27.—*Polyphagus Euglenae*. 1. Young zygote with both nuclei. The male nucleus is still the smaller. 2 to 7. Germination of zygote with a zoosporangium. 8. Empty zoosporangium. (× 670; *after Wager*, 1913.)

thallus always remains unicellular and uninucleate, but in course of time its membrane becomes very firm.

At maturity, on the central sac there appears a spherical outgrowth which increases at about 50μ per hour and develops into a sac about 275μ long. It takes up the whole contents of the mother cell from which it is abjointed. During the vegetative period the original zoospore nucleus has reached dimensions similar to those of *Synchytrium;* it divides repeatedly until several hundred daughter nuclei may be formed. The

chromosome number appears to be from 10 to 12. After cleavage, the uninucleate portions of protoplasm become zoospores liberated by degeneration of the tube.

Polyphagus stands on the dividing line between holocarpism and eucarpism. Physiologically it is still holocarpic. With the formation of the sporangium the plant has spent its life. Morphologically it is already eucarpic, for no longer the whole but only its central portion becomes a sporangium.

At the sudden appearance of unfavorable conditions the single individuals may become encysted so that the central sac is surrounded by a thick membrane. At the return of favorable conditions, they germinate by a sporangium as above described.

If the store of nourishment (fresh *Euglenae*) is exhausted, the plants change to gametangia instead of germinating with sporangia. The smaller, male individual forms a long thin process. On meeting a female cell, this process swells to a sac which thickens its wall echinulately and absorbs the whole content of the male plant. The wall between the female cell and this sac is dissolved and the content of the female cell is discharged into the sac (Fig. 26, 4 and 5). The smaller male and the somewhat larger female nuclei do not fuse but remain diametrically opposite at the periphery. The male nucleus gradually attains the size of the female. Meanwhile the zygote has been separated from the gametangia by two walls, it rounds off and becomes a hypnospore (Fig. 27, 1), while the remains of both plants degenerate. The whole process lasts at most 12 hours.

After a few months the zygote germinates by a zoosporangium into which both sexual nuclei pass and fuse (Fig. 27, 2 and 3), whereupon, possibly, meiosis follows at once. The life cycle may be represented by the following scheme:

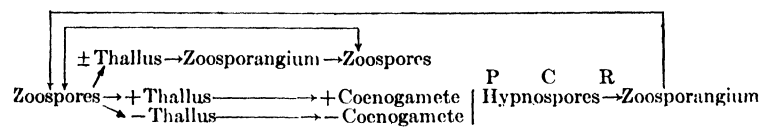


DIAGRAM V.

Thus from one zoospore there arises a unicellular thallus which can form a zoosporangium or a gametangium, with copulation between unicellular coenogametes. In this scheme it is uncertain whether the zoospores throughout the whole period of vegetation may be considered as + and − in the sense of heterothallism, or whether they and their thalli, as assumed in this scheme, are indifferent throughout, with sexual differentiation only in the formation of individuals behaving as gametangia. In contrast to *Olpidium Viciae* (p. 18) the diplont is here reduced to the hypnospore.

Hyphochytriaceae.—In this family, only one form has been described in detail, *Macrochytrium botrydioides* (Minden, 1916), saprophytic on rotting fruits in water. The plants possess a short, almost cylindrical main axis which spreads out at the base in rhizoids, and ends apically with a blunt process. Below the tip, a branch from the main axis swells clavately and later pushes aside the tip. This is abjointed from the rest of the plant, and develops a sporangium (Fig. 28, 1). At its germination, a lid is sharply cut off at the top and the spore mass swells, still surrounded by a membrane (Fig. 28, 2). When the bulging mass has attained about half the size of the sporangium, the membrane ruptures, liberating the uniflagellate zoospores (Fig. 28, 3). Their motion may be amoeboid with the flagellum trailing behind (Fig. 28, 4). Minden considers this a

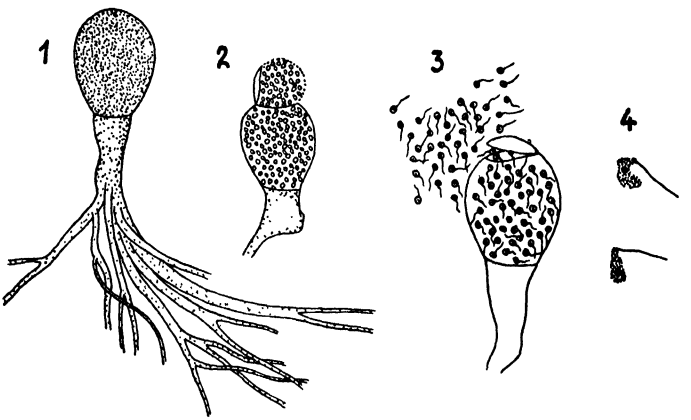


FIG. 28.—*Macrochytrium botrydioides*. 1. Plant with sporangium. 2, 3. Swarming of zoospores. 4. Amoeboid zoospores. (*After Minden*, 1916.)

biological adaptation to their special mode of life, in that often they can reach a substrate covered with other organisms (*e.g.*, bacteria).

Cladochytriaceae.—This family includes a number of saprophytic or parasitic forms which possess an evanescent, very slender, filamentous mycelium with peculiar swellings called **turbinate cells** (Sammelzellen). As a result of this higher stage of development of their thallus they stand far above the other Chytridiales. Since sexual processes, however, have not been demonstrated with certainty, it is still impossible to determine their exact position.

Amoebochytrium rhizidioides (Zopf, 1885), growing in the slime of *Chaetophora*, is transitional between the Rhizideae and this family. The zoospores are aflagellate but capable of amoeboid movement. After they have come to rest, they surround themselves with a membrane and mature to large ramose mycelia. After 36 hours, the hyphae produce peculiar intercalary swellings, rich in protoplasm, which are abjointed

and become flask-shaped sporangia. The marked thickening of their membrane continues beyond the sporangial neck, affects part of the original hyphae and forms a peculiar tube (Fig. 29, 2). The mycelium collapses very early, thereby liberating the sporangia which germinate by a dissolution of the septum in the neck. Hypnospores are unknown.

Cladochytrium and *Nowakowskiella* are somewhat more highly differentiated. In *Cladochytrium* the zoosporangia open by gelification of a papilla, in *Nowakowskiella* by a lid.

Cladochytrium tenue (Nowakowski, 1876) is parasitic or saprophytic in the tissues of aquatic angiosperms, as *Acorus*, *Iris*, *Glyceria*. The mycelium consists of filaments 1 to 2μ thick, which penetrate the infected part of the host intracellularly in all directions and swell up inside the host cells into turbinate cells (Fig. 30, 1). Each changes as a whole into a zoosporangium or is divided by a septum into two daughter cells one or both of which become zoosporangia. Their germination generally takes place through an emission collar which opens into water or into a neighboring host cell and liberates the swarm cells jointed into a sphere. Under special conditions, the sporangia germinate with germ tubes instead of zoospores.

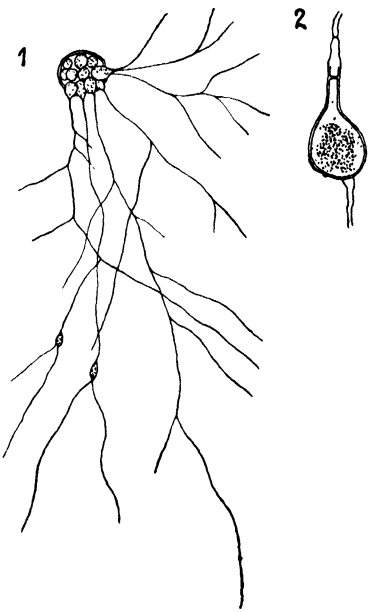


FIG. 29.

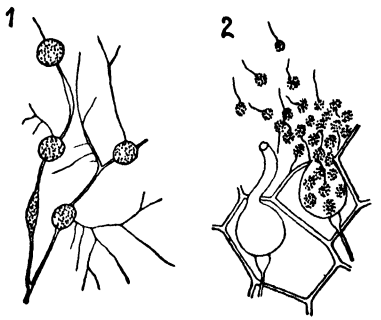


FIG. 30.

FIG. 29.—*Amoebochytrium rhizidioides*. 1. Germ tubes from zoospores which were unable to swarm. Below to the left, two young turbinate cells. 2. Zoosporangium showing thickening of the walls. (*After Zopf*, 1885.)

FIG. 30.—*Cladochytrium tenue*. 1. Mycelium from *Iris pseudacorus* with several turbinate cells which later form zoospores. 2. Germinating and empty zoosporangium. (1 × 400; 2 × 270; *after Nowakowski*, 1876.)

Nowakowskiella ramosa was found by Butler (1907) on decaying wheat stems in India. The mycelium lives both intra- and extramatrically and is unusually well developed for the Chytridiales (Fig. 31, 1). Eight to ten thick-walled hyphae arise from a basal piece; they branch

(so that the places of forking are markedly swollen) and anastomose frequently. The terminal or intercalary sporangia arise by swelling and cutting off hyphal portions; the adjacent hyphal portions swell like apophyses. At germination, a piece of the exospore is thrown off as a lid by the swelling endospore and the uniflagellate zoospores are liberated by a germ sac or singly. In case the sporangia germinate in the interior of a host cell, the wall of the latter is pierced by an emission collar.

In addition to sporangia, hypnospores have also been observed. A certain hypha undergoes longitudinal and transverse divisions so that

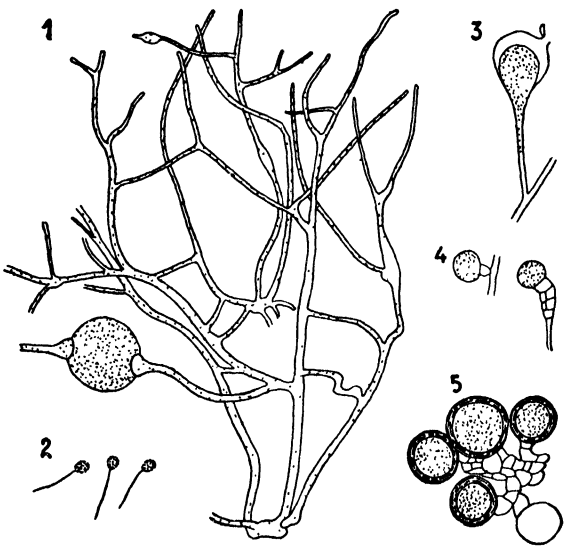


FIG. 31.—*Nowakowskiella ramosa*. 1. Mycelium showing numerous anastomoses and swellings which will later develop zoosporangia. Below to the left, an intercalary zoosporangium with bilateral apophyses. 2. Zoospores. 3. Proliferating zoosporangium, the lid is still visible in the old one. 4, 5. Primordium of hypnospores. (× 608; *after Butler*, 1907.)

the outer cells change to thick-walled spores (Fig. 31, 4 and 5). Their germination is still unknown and their morphological significance still obscure.

Both *Physoderma* and *Urophlyctis* are marked by the high development of their hypnospores which in *Physoderma* are spherical or ellipsoidal, in *Urophlyctis* flattened on one side. The peculiarities of their structure and development have been little investigated, so that their systematic classification offers great difficulties. In numerous species only the hypnospores are known.

In *Physoderma maculare* (*Cladochytrium Alismatis*) on leaves and stems of *Alisma* sp. (Clinton, 1902), the zoospores are uniflagellate;

they come to rest on the young leaves, make a few amoeboid movements and put a short rhizoid into the epidermis. The zoospore body develops shortly into an irregularly indented sporangium, sessile as in *Rhizophidium*. At maturity its content breaks up into numerous zoospores. A part of the walls swells, bursts open and liberates the zoospores. Under favorable conditions, a new sporangium may grow five or six times from the rhizoid into the emptied sheath.

In the formation of hypnospores the content of the zoospores pass over into the rhizoid, which swells up at its end into a small cell. When this is mature, a smaller basal cell is abjointed on the side next the empty



FIG. 32.—*Physoderma Zeae-maydis*. 1. Hyphae with turbinate cells. 2. Mature zoosporangium discharging zoospores by the removal of a lid. 3. Mature zoospore. 4, Amoeboid zoospore. 5. Hyphae with young, binucleate hypnospores. (*After Tisdale*, 1919.)

zoospore membrane. The larger, rich in oil droplets and reserves, is divided into two or more daughter cells; these develop to hyphae which penetrate to neighboring cells of the host and there form similar swellings. On these swellings resting sporangia are formed in a manner as yet unknown.

In *Physoderma Zeae-maydis* which, in North America, causes a disease of maize and teosinte, the hypnospores are liberated as a brown powder in the spring by the rupture of the epidermis of rotting leaves. Their optimum of germination is very high, 26 to 28°. At germination a portion of the exospore is raised like a lid (Fig. 32, 2), the endospore bulges out, finally ruptures and liberates 20 to 50 uniflagellate zoospores. These swim about 1 to 2 hours, come to rest, form amoeboid processes (Fig. 32, 4), surround themselves with a membrane and put forth into the

interior of the host a slender hypha which later branches considerably. The mycelium remains very slender; in the host cells the hyphae swell to turbinate cells (Fig. 32, 1), two to four of which may be joined. Where they are present singly they are rounded up and surrounded by a thick

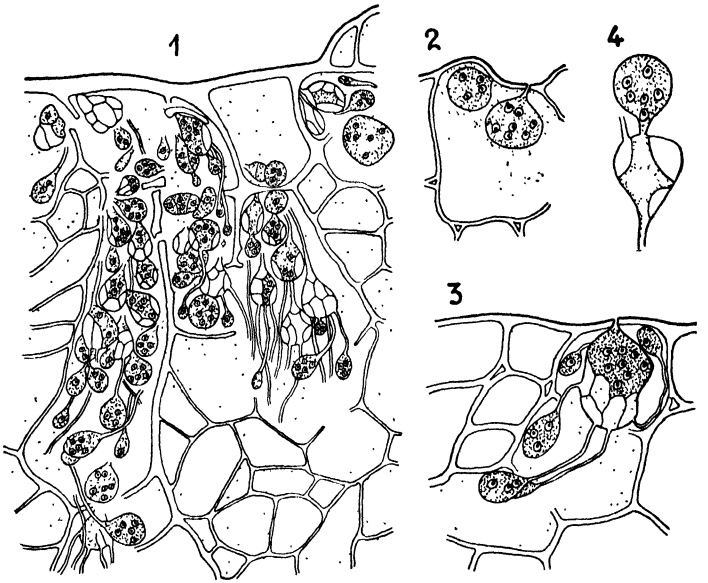


FIG. 33.—*Urophlyctis alfalfae*. 1. Advanced stage of infection of host tissue. 2. Section of an epidermal cell with the primary turbinate cells. 3. Older stage with secondary turbinate cells. 4. Section of a turbinate cell; the nuclei have just migrated from a sporogenous cell into a young hypnospore. 5. A turbinate cell with mature and immature hypnospores. (1 × 280; 2 to 4 × 580; 5 × 560; *after Jones and Drechsler*, 1920.)

wall. In multicellular structures one cell seems to discharge its content into a neighboring cell, which then becomes binucleate (Fig. 32, 5) and forms hypnospores on a lateral process. Further details are still unknown. At maturity the mycelium is entirely disorganised and the hypnospores are left free in the host cell (Tisdale, 1919).

In *Urophlyctis alfalfae* on young shoots of various species of *Medicago*, especially *M. sativa* (Jones and Drechsler, 1920), the germ tube of the zoospores penetrates an epidermal cell and swells to a multinucleate turbinate cell (Fig. 33, 2). Peripheral uninucleate cells are separated from the protoplasm periclinally. Each of these cells develop to a long narrow hypha which later swells terminally into a turbinate cell (Fig.

33, 3) and goes through several nuclear divisions. These processes are repeated (Fig. 33, 1). At maturity the turbinate cells have a crown of filamentous structures which may be regarded as haustoria. The axis of this tuft swells to a sac (Fig. 33, 5) into which the contents of the turbinate cells migrate. There some of the nuclei enlarge markedly and perhaps degenerate. The sac also bears a crown of those peculiar growths; at maturity, its membrane thickens, the growths fall off, the sac becomes a hypnospore and the whole mycelium disintegrates. At germination, the content of the resting spores is divided into a variable number of sporangia (up to 15 or more) which are liberated by regular slits in the wall. There they form emission collars and liberate the uniflagellate zoospores (Scott, 1920).

As related species may be mentioned *U. pulposa* on leaves and stems of *Chenopodium* sp., *U. Trifolii* on the epigaeous ports of *Trifolium* sp., *U. Ruebsameni* on the roots of *Rumex scutatus*, *U. Potteri* (Bartlett, 1926) on *Lotus corniculatus* and *U. pluriannulatus* (Jones and Drechsler, 1920) on *Sanicula Menziesii*.

CHAPTER VIII

OOMYCETES

In the Oomycetes there appears, instead of the uninucleate and centrally organized thallus of the Chytridiales, a well-developed polyenergid mycelium with characteristic hyphae adapted to independent existence. This independence in some families (*e.g.*, the Saprolegniaceae) goes so far that hyphal fragments may grow to new individuals. Furthermore, under unfavorable conditions, smaller portions of hyphae can thicken their walls and become gemmae.

In the lower aquatic forms, asexual reproduction occurs exclusively by zoosporangia with zoospores which may be uni- or biflagellate. In *Ectrogella* and *Saprolegnia*, the zoospores are diplanetic, and in some other genera can shed their membranes. **Diplanetism** is the separation of the swarm period into two morphologically different phases, always in the same sequence, separated from each other by a resting period, while at the shedding of the membrane both swarm phases appear morphologically similar. In diplanetism, the zoospores in the first period may be terminally flagellate, in the second laterally. At the shedding of the membrane, *e.g.*, of a laterally flagellate zoospore, however, the naked protoplasm assumes its previous form, moves out of the membrane and begins a swarm stage (Fig. 39, 3 to 5).

Even in these aquatic forms, at different parts of the system and independent of each other, *e.g.*, *Ancylistes*, *Aplanes*, *Araiospora* and *Pythium*, there is a tendency to allow the zoosporangia to germinate with coenocytic germ tubes intead of with zoospores. As tube germination, in contrast to zoospore germination, can occur in damp air, some of these forms were able to migrate to dry land, where they developed as parasites on phanerogams. Since the highest of these forms have lost their ability to form zoospores, the coenocytic zoosporangia develop directly to coenocytic mycelia.

Along with the decline of differentiation of the sporangial content and the discharge of the unaltered protoplasm into a germ tube, there is a proportional increase in external differentiation of the sporangia themselves. In the lower forms, they are always connected with the sporiferous hyphae and morphologically almost indistinguishable from them, while in the higher forms, they are separated from the hyphae before spore formation, and either fall off and are independently disseminated, or become spores and conidia.

This process of transformation extends also to the sporiferous hyphae. Just as the sporangia lose their sporangial nature and become conidia, the sporiferous hyphae lose their hyphal character and become specialized conidiophores, with limited function. Parallel with this development goes a shifting of the relative values for classification, *e.g.*, in the aquatic forms, as the Saprolegniaceae, the structure of the sporiferous hyphae plays no or only a subordinate part, while in the Peronosporaceae, the form of the conidiophores becomes an important systematic character.

The gametangia are developed as antheridia and oogonia. In the lower forms they arise beside and between the sporangia, and thus show their homology with them. In the Saprolegniaceous *Thraustotheca clavata*, they change to sporangia if they find no mate (Weston, 1918). In the higher forms they are specialized exclusively as sexual organs; in some genera, the oogonia may develop parthenogenetically in the absence of antheridia.

In internal differentiation, there are active morphogenetic forces like those in the zoosporangia. Just as in the latter, the individualization of the uninucleate zoospores is eventually suppressed and the whole content is discharged into a germ tube, so also in the gametangia, after a certain stage, a differentiation into uninucleate male and female gametes is suppressed. The oogonia and antheridia remain coenocytic, the latter germinating with a germ tube instead of with sperms. In the female gametangia, degeneration goes still further; in them a decreasing number of gamete nuclei are admitted for fertilization while the rest degenerate. Around the privileged, sexual nuclei, the protoplasm collects (and this is a specifically new structure for the Oomycetes, giving the group its name) to egg cells (oospheres), to which one or more male cells are attracted and joined by a copulation tube. The fertilized eggs develop to resting spores (oospores). At germination these change into zoosporangia or germinate with germ tubes.

As in *Olpidium* in the Archimycetes and in *Polyphagus* in the Chytridiales, caryogamy does not coincide with plasmogamy, but occurs only at the germination of the zygote, sometimes months after plasmogamy has occurred. Between plasmogamy and caryogamy is inserted a dicaryophase which physiologically is equivalent to the diplophase, but carries the possibility of entirely new developments. We will meet it again in the Zygomycetes.

The classification rests next upon the structure of the zoospores; the uniflagellate and the biflagellate groups are usually treated separately. In the uniflagellate group two families may be distinguished, the Monoblepharidaceae, with hyphae smooth and undifferentiated, and the Blastocladiaceae with constrictions and partial differentiation into main axis and secondary shoots. Furthermore, the Monoblepharidaceae

have fertilization by sperms, while in the Blastocladiaceae the sexual organs are still unknown.

In the biflagellate forms, there are three families: the Ancylistaceae, the Saprolegniaceae and the Peronosporaceae. The Ancylistaceae are

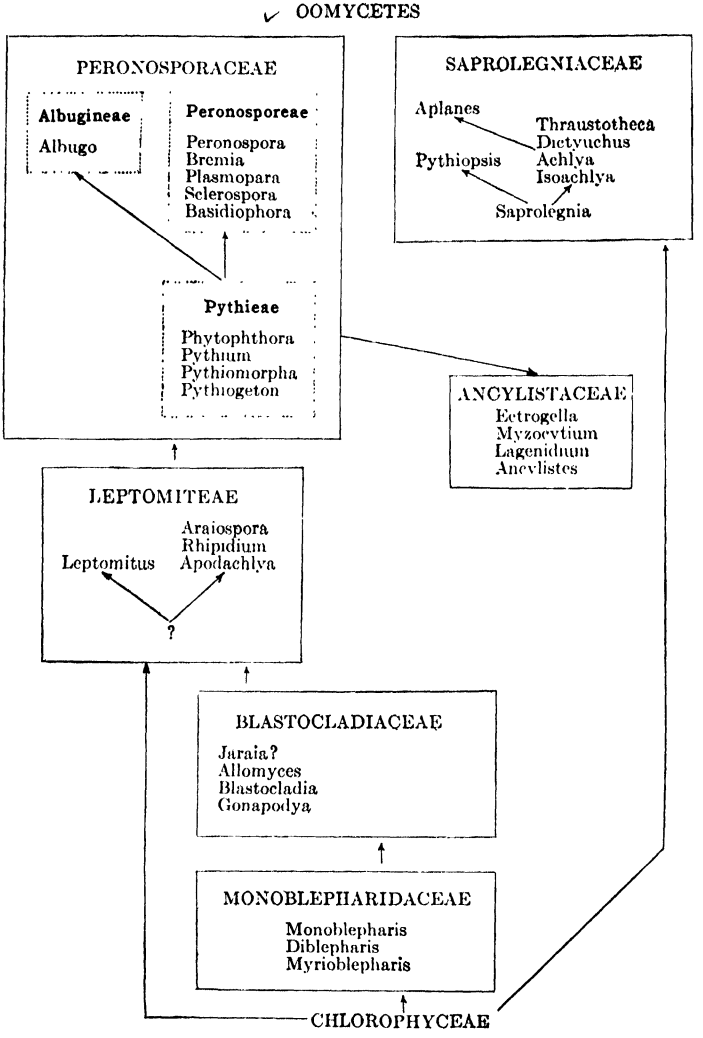


DIAGRAM VI.

aquatic and parasitic on lower plants and animals, their thallus is reduced and limited to the formation of the reproductive organs. At least in *Ancylistes* the contents of the oogonium changes into a single egg cell.

The Saprolegniaceae are also aquatic but are generally saprophytic on animal and plant remains; their thallus is well developed. The oogonial contents collect at the wall, surrounding a large central vacuole, and split into several egg cells. The Peronosporaceae are endoparasitic in land plants. No central vacuole is formed in their oogonia, whose contents are differentiated into a vegetative periplasm and a gonoplasm which forms the single egg.

The morphological relationships between these six families are represented on p. 53. Several parallel developmental series have been distinguished, where *Gonapodya*, *Leptomitus*, *Apodachlya*, *Pythiopsis* and *Achlya* take approximately the same level. On account of the slight differentiation of their oogonia and their diplanetism, the Saprolegniaceae stand at the bottom of the biflagellate series. The Leptomitaceae show great similarities to the Blastocladiaceae. This may be only a convergence phenomenon, as both groups live in stagnant water on decaying objects where other Oomycetes do not appear. Apparently the Peronosporaceae have arisen from Saprolegnioid forms; the organization, however, of the sporangia of the present known genera (as the simpler Pythieae) is lower than that of the modern Saprolegniaceae; on the other hand, the Pythieae, in their zoosporangial germination, still bear traces of earlier diplanetism and roughly correspond with *Achlya*. In this respect they are above *Saprolegnia*. The Ancylistaceae are connected to the Pythieae; both are partially endosparaitic and similar in their habits (Atkinson, 1909*a*). As regards their sexual organs, the Ancylistaceae would be better connected to the present *Saprolegnia*, and below the lowest Pythieae, as their oogonia are more primitive than those of other biflagellate Oomycetes.

A short discussion of the mutual phylogenetic relationships of the Oomycetes, especially the derivation from the green algae, indicated in the scheme on page 53, will be deferred to the close of the order in connection with the Peronosporaceae.

Monoblepharidaceae.—This family occupies a special position in the fungi, because of the motility of its zygotes, elsewhere known only in *Olpidium*, and because of fertilization by motile sperms. *Monoblepharis* is best known. It is found in Europe and North America on fallen twigs in water, especially in spring and fall. The zoospores formed in the spring germinate the following fall, and on twigs which have lain in water all summer, develop a new vegetation whose oospores then winter over and develop further the next spring. In summer they seem suppressed by algae.

The thallus consists of rhizoids which penetrate the substrate, and of multinucleate, little-branched, extramatrical hyphae, only distinguishable from the otherwise similar but thicker hyphae of *Saprolegnia* by their faveolate protoplasm. At the beginning of unfavorable growth condi-

tions, *M. brachyandra* forms moniliform gemmae with thick, brownish walls. Reproduction takes place by zoospores and oogonia with antheridia (Thaxter, 1895; Lagerheim, 1899; Woronin, 1904; Laibach, 1926).

The zoospores develop as follows: In the upper, often somewhat thickened part of a hypha, protoplasm with numerous nuclei collects, and is abjointed from the vacuolate portion. By its cleavage, there are formed one or two series of uninucleate zoospore initials which become zoospores in an unknown manner and swarm through an opening at the tip of the sporangium (Fig. 34, *a*). After some time they come to rest, surround themselves with a membrane and germinate. Subsequently many lateral sporangia may grow out behind each other, so that generally

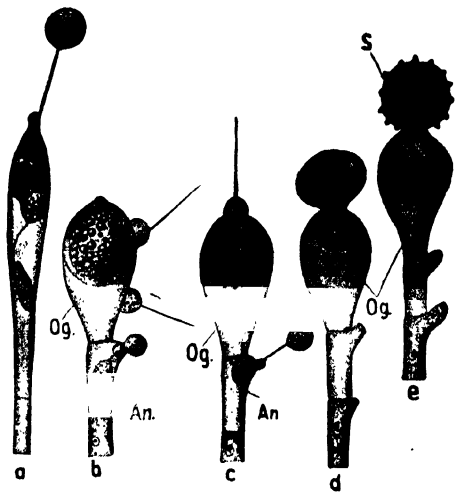


FIG. 34.—*Monoblepharis macrandra*. *a*, Zoosporangium; *M. sphaerica*. *b* to *e*, Fertilization; *Og*, oogonia; *An*, antheridia producing sperms; *S*, oospores. (*After Woronin*, 1904.)

only a portion of the hyphae participates in sporangial formation; thus sporangial conditions result which give the impression of sympodial branching. In other cases proliferation occurs, *i.e.*, a new sporangium arises beneath an old one and grows through its empty membrane.

The antheridia are epigynous in *Monoblepharis insignis*, and *M. brachyandra*, hypogynous in *M. spherica* and *M. macrandra* (Fig. 34, *b*). In the first, the antheridium, like a zoosporangium, is cut off as a terminal cell. The hypha below the septum forms a lateral outgrowth, the neck of the oogonium, and the oogonium itself is abjointed from the rest of the hypha. Thus the antheridium is borne on the oogonium. A new lateral outgrowth develops beneath the oogonium; its tip is separated as an antheridium while the remainder swells to an oogonium and is

abjointed from the sporiferous hypha. This process may be repeated as many as eight times, producing a chain of oogonia, each one of which bears a small antheridium. Sometimes the latter are not formed. In the hypogynous forms, the life cycle is essentially the same, except that the positions of antheridium and oogonium are reversed. In the antheridia as many as 32 sperms, corresponding to the nuclear number, are formed. They resemble zoospores but are only half as large. They swarm through an opening at the tip (Fig. 34, *b* and *c*).

The processes which occur during the development and ripening of the oogonium are not well known. The oogonia are always uninucleate; their protoplasm forms an oosphere. Occasionally they mature later than the antheridia, *e.g.*, *M. brachyandra* is protandrous; consequently self-fertilization is rare, although this species is not self-sterile. The tip of the mature oogonium, which in some species is drawn out into a papilla, gelifies. In *M. insignis* it opens intermittently, permitting part of the substance to escape. The sperms flock together, probably by chemotropism, and by amoeboid motion creep down the neck (Fig. 34, *c*). One of them fuses with the oosphere (plasmogamy). The zeugite then remains at rest. In some exogynous species as *M. brachyandra* and *M. sphaerica* it moves, with revolution and amoeboid alterations of form, to the bottom of the oogonium, and thence again toward the tip whence it escapes (Fig. 34, *d* and *e*). Possibly this motility was caused by the male flagellum being thrown off rather late. Near the opening, it goes through a few amoeboid motions, becomes spherical, surrounds itself with a membrane which gradually thickens and becomes verrucose. In *M. macrandra* it leaves the oogonium entirely by its own motion and matures elsewhere. In the endogenous species, *e.g.*, *M. insignis*, the oosphere remains in the oogonium and is there changed to a hypnospore. Caryogamy takes place comparatively late after the oosphere has left the oogonium, during the formation of the warts. After a rest of several months, germination with meiosis (?) occurs through a germ tube which perhaps develops to a zoosporangium. If the oosphere is not fertilized, it is surrounded in the oogonium by a membrane and develops parthenogenetically to a hypnospore. Conversely sperm fertilization admits the possibility of cross fertilization; thus Woronin considers *M. macrandra*, var. *longicollis*, a hybrid between *M. polymorpha* and *M. spherica*.

Two other genera which have been important in the discussion of the significance of the flagella for classification, *Diblepharis* with biflagellate zoospores, and *Myrioblepharis* with multiflagellate zoospores, should be considered in this family. In fitting the facts to the classification, Woronin (1904) suggests the possibility that the biflagellate zoospores belong to a parasite which has penetrated; in the second, Minden (1915) suggests a mixture of *Pythium* and protozoa.

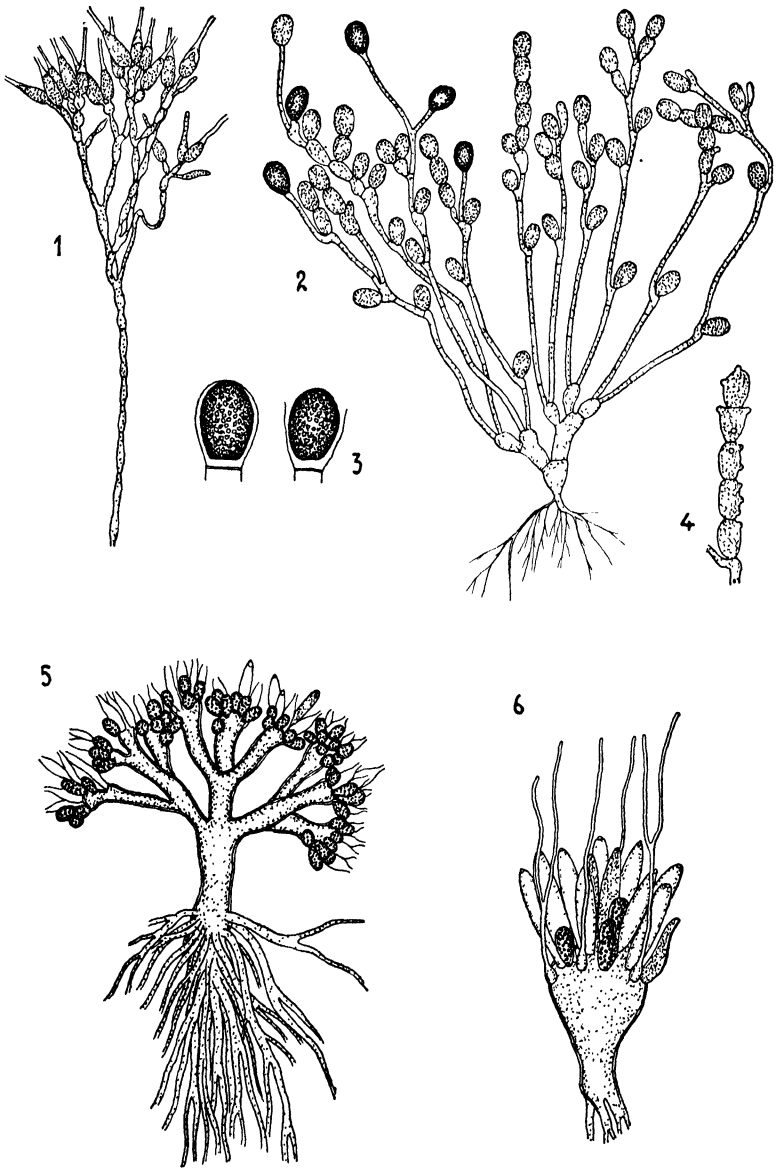


FIG. 35.—*Gonapodya siliquiformis*. 1. Hyphae with proliferating zoosporangia. *Allomyces arbuscula*. 2. Plants with rhizoids, zoosporangia and some hypnospores. 3. Hypnospores. 4. Chain of mature zoosporangia which have formed germ papillae. *Blastocladia Pringsheimii*. 5. Plant, bearing sporangia and hypnospores. 6. Detail showing hair formation. (*After Minden*, 1916; *Butler*, 1911.)

Blastocladiaceae.—In the differentiation of the thallus into principal and secondary axes, this family is reminiscent of the Leptomitaceae, from which it differs by its typical uniflagellate zoospores. As sexual organs are unknown, its systematic position and classification are still obscure.

In *Gonapodya siliquiformis* and *G. polymorpha*, on fruit and twigs lying in water, the mycelium is differentiated into principal and secondary axes (often indefinitely); the individual hyphae are divided by slight constrictions into more or less easily visible segments (Fig. 35, 1). The sporangia are terminal and ovoid and renew by proliferation. They open by an apical pore through which the zoospores pass out singly and swarm or creep away. The systematic position of this genus is doubtful, as zoospores of varied size and flagellar number have been reported in *G. polymorpha*.

The other genera, also saprophytic and aquatic, are characterized by the differentiation of its thallus into a highly developed basal cell attached to the substrate by rhizoids and into true hyphae growing from the basal cell and generally ending in sporangia (Fig. 35, 2). The basal cell corresponds essentially to the turbinate cells of the Cladochytriaceae; it arises from the body of a germinating zoospore while its germ tube develops to a rhizoid system. The sporangia are mostly solitary and terminal, in *Allomyces* also occasionally moniliform. Their content is split directly into single zoospore initials as in *Monoblepharis*, *i.e.*, without the formation of a large central vacuole. Germination of most species takes place slowly in the form of a sac out of which the zoospores swarm. They generally creep around like amoebae. The number of their flagella varies from one to three, but in typical cases is one.

In *Allomyces arbuscula* (*Blastocladia strangulata*) the zoosporangial branches still have constrictions as in *Gonapodya* (Butler, 1911; Barrett, 1912; Kanouse, 1927). In these constrictions several broad trabeculae, which permit a free circulation of cytoplasm are formed centripetally from the wall, chiefly in age and upon damage to the hyphae fuse into a false septum. The sporangia are ovoid with several emission collars. In forma *dichotoma* (*Septocladia dichotoma*) the constrictions are absent (Coker and Grant, 1922; Kanouse, 1927).

In *Mindeniella spinospora* (Kanouse, 1927) the sporangia and oogonia are pedicellate and the oogonial walls echinulate.

In *Blastocladia*, the false septa of trabeculae are absent and the sporangia are cylindrical with one emission collar. In *B. prolifera*, the sporangia proliferate as in *Saprolegnia*. The basal cell in *B. ramosa*, *B. gracilis* and *B. tenuis* is cylindrical and dichotomously branched, in *B. globosa* is subspherical, in *B. rostrata B. Pringsheimii* and *B. prolifera* is variously branched. In *B. globosa*, antheridial branches have been reported by Kanouse (1927) but the process of fertilization was not observed. Since

these branches are rare, she suggests that the oospores probably develop parthenogenetically.

In addition to the sporangia, characteristic hypnospores, which fall off at maturity and leave scars on the sporangiophores, have been observed, *e.g.*, in *B. Pringsheimii* (Fig. 35, 5). In *Allomyces arbuscula* these hypnospores arise inside the terminal segment (Fig. 35, 3). Their morphological significance is still puzzling. Butler (1911) regards them as parthenogenetically developed oospores which find their analogues in the endogenous species of *Monoblepharis*.

Finally the only parasite in this group, *Jaraia Salicis* (Němec, 1911), on root tips of *Salix purpurea* in Czechoslovakia, lacks differentiation into primary and secondary shoots, and segmentation of the sporiferous hyphae. It possesses antheridia and oogonia; in the latter there arise as many as 50 rather thin-walled zoospores. Further investigation would give interesting results.

Ancylistaceae.—At present only aquatic forms on pollen grains, algae and animals are known. Because of their simple thallus and holocarpy, some authors place them in the Chytridiales; however, since they form oospores, they undoubtedly belong to the Oomycetes. Here also relationships are obscure, particularly because the exact processes before and after fertilization are insufficiently known. They are considered by A. Fischer (1882), Schroeter and Scherffel (1925) as ascending forms which lead from the Archimycetes and Chytridiales to the Oomycetes. Scherffel bases this conception on his observations concerning the diplanetism of *Ectrogella*, which he connects directly to the shedding of the membrane as described for *Phlyctidium* (p. 36). It is a question whether *Ectrogella* forms true oospores or whether it does not rather behave as *Zygorhizium*, *Pseudolpidiopsis*, etc. (empty appendiculate cells in *E. Licmophorae!*). Further, their zoospores are not reniform with a true lateral insertion of flagella, as in the true Ancylistaceae, but pyriform with more or less terminal flagella. Hence it is quite possible that *Ectrogella* does not belong to the Oomycetes and, in spite of its two flagella, should be classified with the Chytridiales. In this case, the main support for deriving the Ancylistales from the Chytridiales would be removed; also *Ectrogella* would take a more significant position in the Chytridiales as it would explain the peculiar collecting of zoospores at the mouth of the emission collar.

Bary and Tavel, on the other hand, regard the Ancylistaceae as simple or simplified Pythiaceae. This conception appears nearer the truth, as in the better-known genera, with the exception of *Ectrogella*, the zoospores possess laterally inserted flagella. I prefer not to regard them an ascending line, as one cannot imagine how the less complex soil saprophytes, like the *Aphragmium* group of *Pythium*, have arisen from such parasites as *Ancylistes* and *Myzocytium;* but I prefer to consider

them a line gradually degenerated as a result of submersed parasitism. Hence the individual genera are considered in a series, descending in respect to zoospore germination: first *Myzocytium*, in which zoospore initials still arise within the sporangium, pass out as such into the germ sac and there develop their flagella; then *Lagenidium*, in which the protoplasm partly flows out in a continuous stream through the emission collar into the germ sac, and only there differentiates into the individual spore portions; and finally *Ancylistes* where there is no differentiation of zoospores and the emission collar, as the infection tube seizes new hosts. These true Ancylistaceae are placed before *Ectrogella*.

The better-known species of *Ectrogella* parasitize algae. The commonest species, *E. Bacillariacearum* on diatoms, chiefly on *Synedra*, is psychrophilic and occurs chiefly in spring and late fall. When a zoospore reaches a host, it surrounds itself with a wall, and forces its germ tube into a raphe. The thallus in time increases much in volume and forces the valves of the diatom apart. The protoplasm of the whole mature thallus collects at the wall (as in *Olpidiopsis* and the Saprolegniaceae) and splits into zoospores which are liberated by a short, papilliform emission collar. The zoospores have two short flagella of equal length inserted in a lateral depression below the tip; thus they are isocont. After a short, not very intensive swarm stage, they come to rest and surround themselves with a wall. Later, in the form of secondary zoospores, they again slip out of this wall which they leave behind as an empty sheath. Thereafter they possess a long and a short flagellum (and thus are heterocont) and are very actively motile.

In other species, as in *E. monostoma* and *E. Licmophorae*, the first swarm stage is considerably shortened. The primary zoospores collect before the emission collar into a moriform group, shed their membranes and swim away as secondary zoospores. Unfortunately these relationships cannot be given diagrammatically in this book, as the work of Scherffel only appeared after the figures were finished. One can picture them approximately, however, if one imagines in Fig. 36, 9, a group of empty zoospore membranes before the emission collar, as shown for *Achlya racemosa* (Fig. 39, 1).

E. monostoma and *E. Licmophorae* are thus related to *E. Bacillariacearum*, as in the Saprolegniaceae *Achlya* is to *Saprolegnia*. In *E. Bacillariacearum*, the shedding of the membrane of the primary zoospores occurs as in *Saprotegnia*, far from the zoosporangium; in *E. monostoma* and *E. Licmophorae*, as in *Achlya*, directly before its opening.

This parallelism to the Saprolegniae goes farther in *Ectrogella* for in *E. Dicksonii* (*Eurychasma Dicksonii*, *Rhizophidium Dicksonii*), the shedding of zoospore walls may take place in the interior of the zoosporangium, thus leaving the empty walls inside the zoosporangium, as in the net sporangium of *Dictyuchus*.

Unfortunately in the aquatic Chytridiales, no studies of this sort have been carefully conducted, but the conjecture of Scherffel, that an entirely new point of view will be found, seems to be entirely justified.

In *Myzocytium proliferum* on Zygnemaceae and *M. vermicolum* on anguillules (Zopf, 1885; Dangeard, 1906), the zoospores are slightly reniform and possess two lateral flagella. During their swarm period they undergo amoeboid alterations of form. They then come to rest,

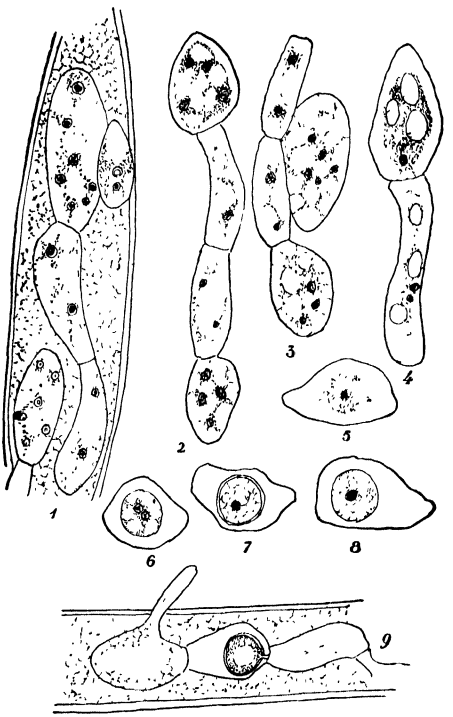


FIG. 36.—*Myzocytium vermicolum*. 1. Worm with two specimens of parasite. 2. Cell filament with two antheridia in the middle and an oogonium at each end. 3, 4. Antheridia and oogonia. 5 to 8. Development of oospores. 9. Individual oospore in worm. (*After Dangeard*, 1906.)

surround themselves with membrane, force a germ tube into the host cell and there mature to a thick, cellular multinucleate mycelium. At the beginning of the formation of the fructification, the whole mycelium is divided by septa into multinucleate members, each of which becomes a zoosporangium (Fig. 36, 1). The protoplasm collects at the walls and splits into uninucleate zoospore initials which pass singly out through an emission collar and assemble at its mouth in a sac. Soon the flagella are visible, the sac bursts, and the zoospores swarm. Zoospores which

do not find an exit and remain in the zoosporangium may germinate there and pierce the walls.

At the appearance of unfavorable conditions, antheridia and oogonia are formed in some segments instead of sporangia (Fig. 36, 2 to 4). The antheridium remains cylindrical and contains few, often only two, nuclei. The oogonia swell and become barrel shaped; usually there are about eight nuclei. At maturity all female nuclei except one degenerate; it is still uncertain whether this lies in a special oosphere. A neighboring antheridium, generally of the same, rarely of another plant, forces a copulation tube through the wall of the oogonium, into which a single nucleus migrates and soon fuses with the female nucleus. An oospore

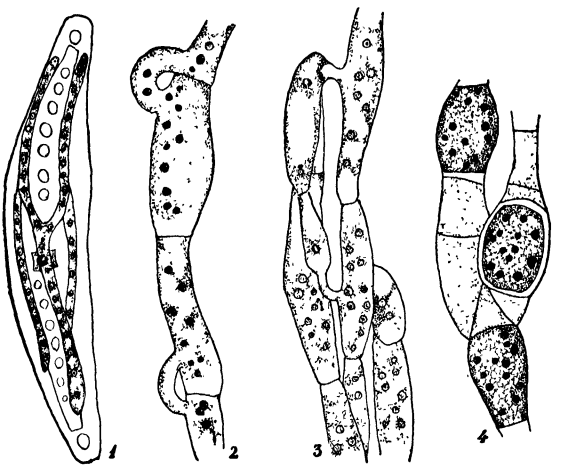


FIG. 37.—*Ancylistes Closterii*. 1. *Closterium* with parasite. 2, 3. Fertilization. 4. Mature zoospores. (*After Dangeard*, 1906.)

with a double wall develops and probably germinates by zoospores which escape through the neck.

Lagenidium Rabenhorstii (Zopf, 1885), causing an epidemic on the mats of *Spirogyra*, *Mesocarpus*, etc., and *L. pygmaeum* (Zopf, 1888) on *Pinus* pollen in water, agree essentially with *Myzocytium*, except that their mycelium is lobulate. The sporangia discharge undifferentiated protoplasm into a germ sac formed at the mouth of the emission collar. The sac begins to rotate, bursts and liberates the biflagellate zoospores. Occasionally in *L. americanum* there is no differentiation into zoospores, but the naked protoplasm swims away with many flagella (Atkinson, 1909).

In *Ancylistes Closterii* on *Closterium*, the emission collar develops to a regular hypha into which the sporangia discharge their whole content. From time to time they are abjointed in the rear from the

empty part. Thus the formation of zoospores is entirely suppressed and the undifferentiated sporangium germinates by a mycelial filament. Wherever this comes in contact with a *Closterium* it pierces the wall and grows into the interior. *A. Closterii* is generally dioecious. As in *Myzocytium*, there are few nuclei in the antheridium but many in the oogonium. They divide in the mature sexual organs. Then the antheridia form copulation tubes (Fig. 37, 2 and 3) through which the whole content migrates into the oogonium. The details of development and the germination of the oospores are not yet known, it is particularly uncertain whether nuclear fusion occurs between all nuclei or, as in *Myzocytium*, between privileged nuclei.



FIG. 38.—*Saprolegnia*. Development of zoospores. *A*, Young zoosporangium whose peripheral protoplasm has a large number of nuclei· *B*, (section) uninucleate spore initials are formed in the peripheral layer by radial cleavage; *C*, *D*, spore initials contract, separate and round up. (*After Davis*, 1903.)

Saprolegniaceae.—This family is mostly saprophytic, rarely parasitic on plant and animal substrates in water and soil. The mycelium is tubular, generally differentiated into slender, ramose, intramatrical hyphae and into thick, less-branched extramatrical hyphae, up to 200μ in diameter. The vacuolate protoplasm lies next the wall. Under favorable conditions, the resting hyphae change to gemmae. The hyphal tip swells to a short clavate organ stored with protoplasm, is abjointed, rounds off and thickens its wall. This process is repeated basipetally, so that a moniliform chain results.

When the extramatrical hyphae have attained a certain age, their ends become clavate or spherical, filled with thick protoplasm and numerous nuclei, and are abjointed as zoosporangia (Rothert, 1892). The peripheral protoplasm splits without further nuclear division into

uninucleate portions (Fig. 38 *A* and *B*); these round off, acquire two flagella and swarm (Trow, 1899; Davis, 1903). In many forms (as in many species of *Saprolegnia* and *Leptolegnia*) the adjacent portion of the hypha penetrates the empty sporangium and there swells up or, if it has grown through the sporangium, it forms a second sporangium at its tip. This may be repeated several times. In other genera, as in *Achlya*, *Aphanomyces* and *Pythiopsis*, the sporangia are renewed by lateral outgrowth of a portion of the hypha next the empty sporangium. There, too, the process may be repeated, forming sympodially divided, verticillately or spirally arranged sporangia. In still other forms as *Saprolegnia torulosa*, and some species of *Pythiopsis* and *Dictyuchus*, the sporangia may be intercalary, catenulate or occasionally intermingled with oogonia.

The behavior of swarming zoospores is very different in different genera. In *Saprolegnia*, they are ovoid (Fig. 4, s^2) with two flagella at the pointed ends. After a time they come to rest and surround themselves with a cellulose wall. They do not put forth a germ tube, but their naked protoplasm slips out of the wall as a reniform swarm spore with two flagella in a lateral indentation. The empty sheath degenerates. Generally the second swarm stage lasts longer than the first. When it ends, the zoospores are again surrounded by a wall and develop to a mycelium.

This diplanetic basic form of the *Saprolegnia* type has been modified in the various genera by a suppression of one or both swarm stages. In *Pythiopsis*, the second swarm stage has disappeared, its zoospores come to rest immediately after the stage with two apical flagella and germinate with a hypha. In the *Achlya–Thraustotheca* series, as in the *Ectrogella Bacillariacearum* and *E. Dicksonii* series, the first stage is gradually suppressed. In *Achlya* (Fig. 39, 1), *Plectospira* (Drechsler, 1927) and *Aphanomyces*, the generally aflagellate zoospore initials (in some species they still seem to possess two terminal flagella) form a small cluster in front of the sporangial opening, shed their walls and swarm as reniform zoospores with lateral flagella, leaving the group of empty sheaths before the opening of the sporangium. In *Dictyuchus*, the zoospore initials no longer come out but surround themselves, while still in the sporangium, by a membrane out of which the spores swarm singly through an opening in the sporangial wall. The empty spore membranes remaining behind in the sporangium thus form a delicate, transient, net sporangium. In *Thraustotheca*, the zoospores, surrounded by a membrane, are liberated through a rupture in the sporangial wall or by its destruction (Fig. 39, 6). There, according to circumstances, they germinate with a laterally flagellate zoospore, a mycelium or a sporangium.

In other forms, reduction has also affected the second swarm stage; thus in *Achlya aplanes* (Maurizio, 1894) the zoospore initials come out

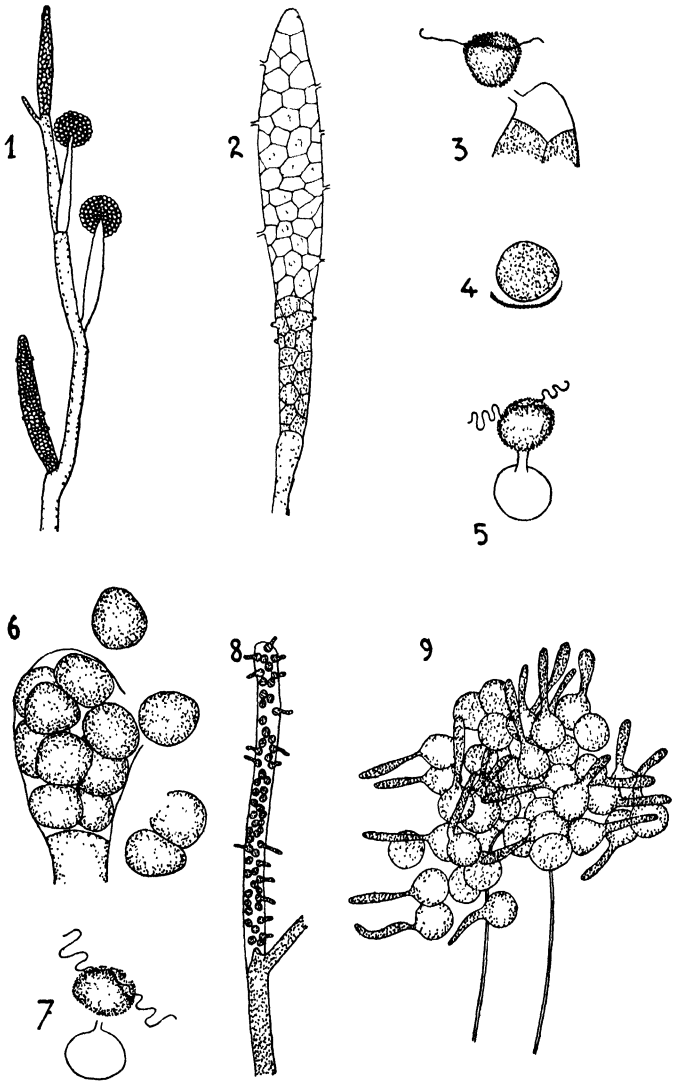


FIG. 39.—Saprolegnieae. Degeneration of diplanetic zoospores. 1. *Achlya racemosa*. Sporangiferous hyphae. Both upper sporangia are empty while the lower contains zoospores already surrounded by a membrane (Reticulate sporangium). 2. *Dictyuchus monosporus*. Two superimposed zoosporangia, with reticulate structure, the upper empty, the lower just mature. 3. Exit of zoospore from zoosporangium. 4. Zoospore surrounded by membrane. 5. Resting zoospore has just slipped out of membrane. 6. *Thraustotheca clavata*. Liberation of sporangiospore balls. 7. Exit of zoospore from sporangiospore. 8. *Aplanes Braunii*. Sporangium with internally germinating zoospores. 9. Germination of zoospores before zoosporangium, 10 hours after their exit. (1 × 55, 2 × 370; 3 to 7 × 930; 8 × 33; 9 × 280; *after Pringsheim, Weston, Bary and Maurizio.*)

before the sporangial opening and are there surrounded by a membrane. No shedding of the membrane follows, and the resting zoospores germinate directly to a mycelium (Fig. 39, 9). This emission of naked protoplasmic portions is reminiscent of diplanetism; but this character too disappears. In *Aplanes* the zoospore initials, while still in the sporangium, surround themselves with a wall and germinate there, piercing the sporangial wall with their germ tubes (Fig. 39, 8). In *Geolegnia*, the zoospore initials surround themselves with a thick wall and await the decay of the sporangial wall before germinating directly to mycelium (Harvey, 1925). Thus zoospore formation is entirely suppressed. It is noteworthy that these degenerate, functionless sporangia only appear occasionally in the mats; they are replaced by sexual reproduction. Thus *Aplanes* and *Geolegnia* seem to be on the point of entirely giving up degenerate asexual reproduction in favor of sexual.

The sexual organs are developed (as in the Ancylistaceae) as antheridia and oogonia. In *Saprolegnia mixta* (Klebs, 1889) and *Achlya radiosa* (*A. decorata*) (Obel, 1910), their formation may be hastened by lowering the concentration of the medium or by lack of phosphates. Couch (1926) reports *Dictyuchus* is heterothallic, physiologically differentiated strains being necessary to secure production of antheridia and oogonia. The oogonia generally arise terminally on short branches of the main hypha, more seldom intercalary or incased in empty sporangia. Their wall is generally thicker than that of the vegetative hyphae, colorless or yellowish, smooth or covered with stellate projections. The antheridia develop on branches which are more slender and branched than the oogoniophores. If the antheridiophores arise on the same hyphae as the oogonia which they fertilize, the form is called **androgynous**, if they arise on other hyphae, they are called **diclinous.** Whether androgyny and diclinism correspond to true heterothallism still remains to be investigated. Homothallism has been definitely proved only for the androgynous *S. monoica* (Kniep, 1919). In certain species, the antheridia arise directly under the oogonia and on the same hypha (hypogyny). In still other species, they are entirely lacking or no longer functional, and the oospores develop parthenogenetically. Klebs (1899) and Kauffman (1908) determined that the forms of development may be entirely influenced by the chemical character of the nutrient solution; thus *S. hypogyna*, which normally forms hypogynous antheridia, may form them on branches in certain nutrient solutions.

Dangeard (1891) and Claussen (1908) studied the ontogeny of *S. monoica* and Davis (1903) the oogonia of *S. mixta.* The antheridia and oogonia take large masses of nuclei from the hyphae and then are abjointed from the remaining part, the stipe. Before the septum is completed, the cytoplasm and nuclei degenerate in the oogonium, progressively from the center toward the periphery. This process continues

until only a thin protoplasmic wall layer with few nuclei remains (Fig. 40, *A*). The nuclei then undergo simultaneously a single mitotic division and degenerate; finally the protoplasm splits, rolls up around each of the remaining nuclei and forms uninucleate eggs, oospheres (Fig. 40, *D*). At first the egg nucleus shows a rostrate process with a definite centrosome.

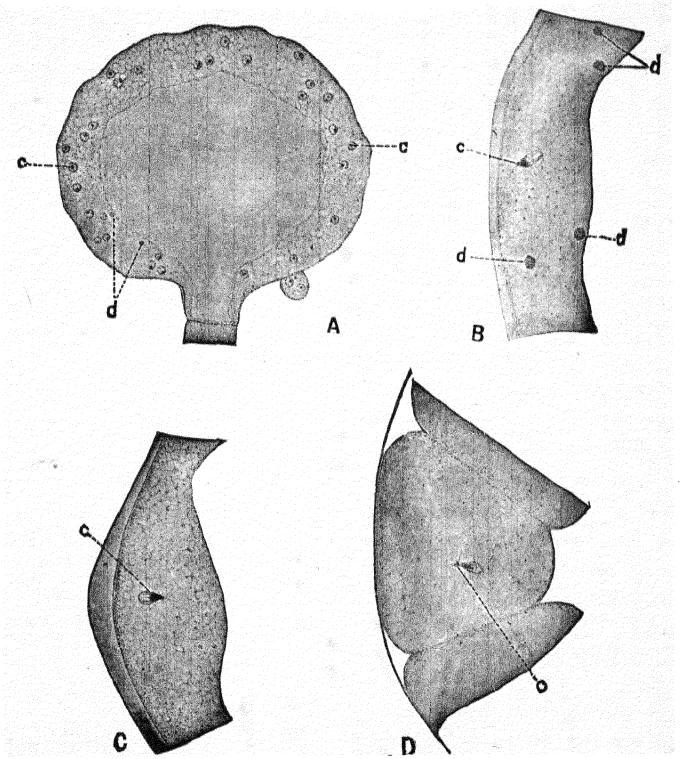


FIG. 40.—*Saprolegnia monoica*. Egg development. *A*, young oogonium with peripheral protoplasm; *B* to *D*, sections of the peripheral layer in different stages of development; *c*, normal nucleus with centrosomes; *d*, degenerating nuclei. (*After Claussen*, 1908.)

Meanwhile the antheridium has approached the oogonium and partially surrounded it. About simultaneously with that of the oogonium, the nuclei divide once. Hereupon the antheridia pierce the oogonial membrane through pits. Within the oogonium the process divides into several branches, each of which approaches an egg cell and discharges a nucleus into it. Nuclear fusion follows immediately. The fertilized egg surrounds itself with a two-layered, smooth, colorless membrane: it becomes an oospore with the character of a hypnospore.

In contrast to the Ancylistaceae, a new structure has arisen, especially in the female gametangium. Its content is no longer changed into a single multinucleate egg, but, as in the primitive gametangium, it is split into uninucleate daughter cells, here called **oospheres.** These may not be considered homologous to true female gametes, however, for their nuclei only represent the remaining privileged sexual nuclei. Morphologically the eggs are coenocytic; functionally, however, the female gametes have recovered atavistically to a certain degree their earlier individuality; to be sure, they no longer swarm, but each acquires a male nucleus for itself through a special branch of the fertilization tube. The process is the same as in *Olpidium* in which (if one considers them heterogamous) several sexual acts occur between the gametes of two gametangia and several zygotes result. In the Saprolegniaceae a number of sexual acts between the two gametes of two gametangia occur and many zygotes (oospores) result; only the male gametes are no longer recognizable as individuals and the female gametes always remain in the gametangia; thus the sexual acts are shifted back to the female gametangia where the zygotes remain enclosed.

After maturity of the oospores, the oogonia remain connected with the mycelium until it disintegrates; much later they, too, degenerate so that the oospores are liberated and germinate. Usually after a rest of 2 to 5 months, germination takes place with a germ tube where meiosis occurs. According to the nutrient content of the environment, it ends in a sporangium after a short time or develops to a mycelium. The rest period does not seem indispensable in all species; thus, in *S. mixta*, it may be shortened to 8 to 10 days by placing the oospores in pure water at 23 to 25°.

Achlya americana (Trow, 1899), *A. debaryana* (Trow, 1904), *A. polyandra* (Mücke, 1908) and *Plectospira myriandra* (Drechsler, 1927) agree essentially with *Saprolegnia monoica* in reproductive processes, as far as they have been studied. In *A. americana*, Trow first observed meiosis in the germination of the oospores, finding four chromosomes in the nuclear figures and eight in the first division of the zygote nucleus. In *Aphanomyces laevis* (Dangeard, 1891; Kasanovski, 1911), there is a notable reduction which is reminiscent of the relationships in *Myzocytium* and in the Peronosporaceae. After mitosis all the oogonial nuclei degenerate except one, the future egg nucleus. The single egg results from the protoplasm rounding up gradually in the interior and consuming all the protoplasm contiguous to the wall. In the center of the egg is a thick, deeply staining bit of protoplasm which probably corresponds to the coenocentrum (coenosphere) of the Peronosporaceae. In the antheridium, also, all nuclei but one degenerate; this, together with the protoplasm, penetrates the oogonium through a copulation tube and fuses

with the female nucleus. The mature oospore is uninucleate. After a resting period of 6 months, it develops a germ tube.

If we consider the life cycle of the Saprolegniaceae from the point of view of nuclear phase, we get the following picture:

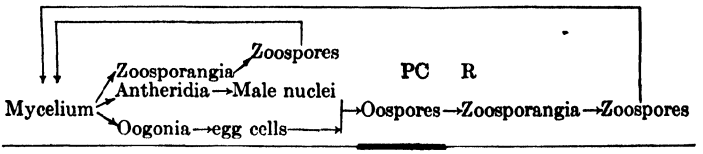


DIAGRAM VII.

This scheme corresponds essentially with that of *Polyphagus Euglenae* (p. 44) if one ignores the complication caused by heterothallism in the latter. The differentiations caused by the development of the mycelium in form and function of the haplont, have been discussed in the introduction to the Oomycetes (p. 51).

Saprolegnia is saprophytic on animal cadavers in all sorts of water, occasionally, parasitic on living fish, whose eggs it may infect and thus cause extensive epidemics. As far as is known, the infection is preceded by a weakening or injury of the individuals infected. The genus includes about 30 species which are chiefly distinguished by the structure and arrangement of the sexual organs; the value of these specific characters should be more thoroughly studied as its habit is extensively influenced by nutritive conditions. The same species occur in Europe and North America, as *S. dioica*, *S. monoica*, *S. mixta* and *S. ferax* (*S. Thureti*) (Humphrey, 1892; Coker, 1923). Some of them appear in the Alps and in Lapland beyond the borders of the snow (Tiesenhausen, 1912; Gäumann, 1918). *S. anisospora* forms two kinds of zoospores like *Gonapodya*, a smaller typical form and a larger, more than double the size of the smaller, with dark-brown protoplasm. There are transitional types; but one sporangium contains spores of one type only. Whether this phenomenon has a special significance is still unknown.

Achlya polyandra of Europe and *A. racemosa* of North America behave like *Saprolegnia*. In *Protoachlya* we have a transition from *Saprolegnia* to *Achlya*, as in *P. paradoxa* whose form and sporangial arrangement agree with *Achlya* and whose diplanetism resembles that in *Saprolegnia* (Coker, 1914; 1923). *Isoachlya* is similar but all the zoospores are motile, the oogonia are often in chains and the antheridia are rare (Kauffman, 1921; Coker, 1923).

In *Aphanomyces*, which differs from *Achlya* in its long fusiform sporangia, *A. laevis* causes a root blight of sugar beets and *A. euteiches* (Jones and Drechsler, 1925) a root rot of peas. *Plectospira myriandra* produces injury of tomato rootlets.

Leptomitaceae.—In the structure of their thallus, this family probably forms a considerably modified series parallel to the Saprolegnieae, and to the uniflagellate Blastocladiaceae. All species so far known are aquatic.

One of the simpler species is *Leptomitus lacteus*, saprophytic in sewage rich in nitrogen. It covers everything with a dirty white, slimy coat, and in luxuriant development the mycelial masses become loosened in clumps, move away and collect in quiet spots where their mass and rapid decomposition cause trouble. The mycelium is ramose, the main axes are at times better developed. As in *Gonapodya* of the Blastocladiaceae (Fig. 35, 1), the main axis and branches are generally divided into segments by constrictions. Each segment contains one or more granules

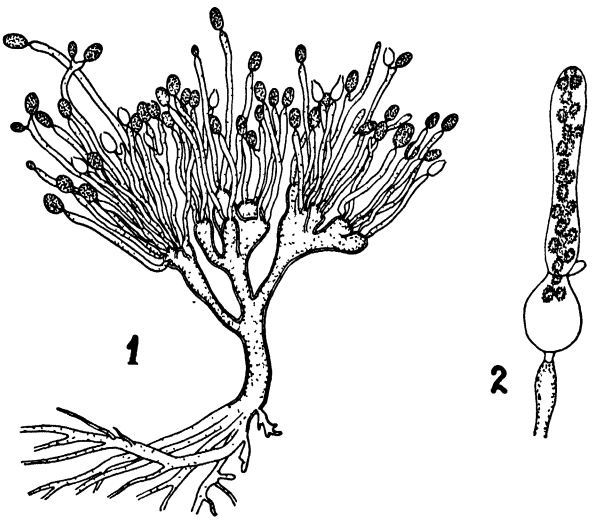


FIG. 41.—*Rhipidium europaeum*. 1. Plant with zoosporangia. 2. Zoosporangium during exit of spores. (*After Minden*, 1916.)

of cellulin, a carbohydrate probably closely allied to cellulose: it is still unknown whether these granules serve as reserve materials or as plugs, because if they reach a stricture, they swell and fuse with the membrane so that a septum-like valve is formed. In this manner, a septation of the mycelium may be simulated. The sporangia correspond to segments and are sometimes formed in short chains. The zoospores are ovoid and, as in *Pythiopsis* of the Saprolegniaceae, possess two apical flagella. They often escape through a lateral pore. Sexual organs have not yet been found; under unfavorable conditions, however, gemmae are formed.

The species of *Apodachlya* as *A. pyrifera*, on rotting plant substrates, agree in habit with *Leptomitus*, and like *Achlya* can renew sporangia by lateral sprouting. In the germination of their sporangia they are also

reminiscent of the *Achlya* type; the zoospore initials pass out through an emission collar, collect before its opening in the form of a hollow sphere and surround themselves with a membrane. After a short time they slip out and, leaving behind the empty sheath, swarm away as reniform, laterally flagellate zoospores. Occasionally they do not shed the membrane so that the zoospores of the second swarm stage arise directly in the sporangium. Sexual organs have not yet been determined with certainty.

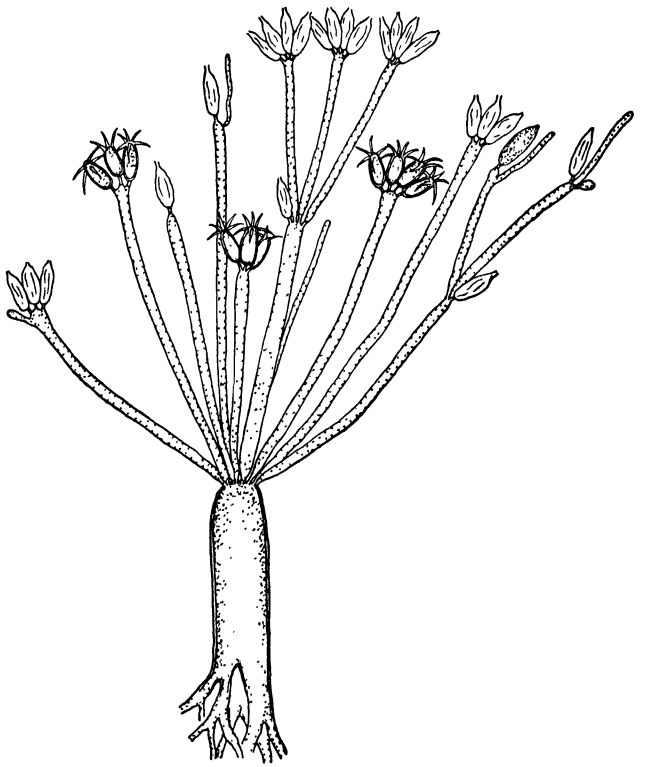


FIG. 42.—*Araiospora spinosa*. Plant with simple and echinate sporangia. (*After Minden*, 1916.)

In *Rhiphidium* and *Araiospora* both of which (like *Apodachlya*) possess laterally flagellate zoospores, the main axis is shortened and becomes a voluminous broad cylinder which bears a tuft of auxiliary axes. These axes may terminate in a sporangium or branch terminally like the main axis.

The species of *Rhiphidium*, as *R. europaeum*, live on rotting fruits and fallen twigs in water. Their mycelium is reminiscent of *Allomyces* (Fig. 35, 2); it consists of a very large thick-walled basal cell

whose much-branched rhizoids are rooted in the substrate and bear on apical lobate processes, numerous thin, generally unbranched, hyphae which usually end with a sporangium (Fig. 41, 1). The zoospores arise, as in the Saprolegnieae, from peripheral protoplasm, shortly before evacuation the inner layer of the sporangial walls swells. The outer cuticular membrane is separated as a small lid at the top of the sporan-

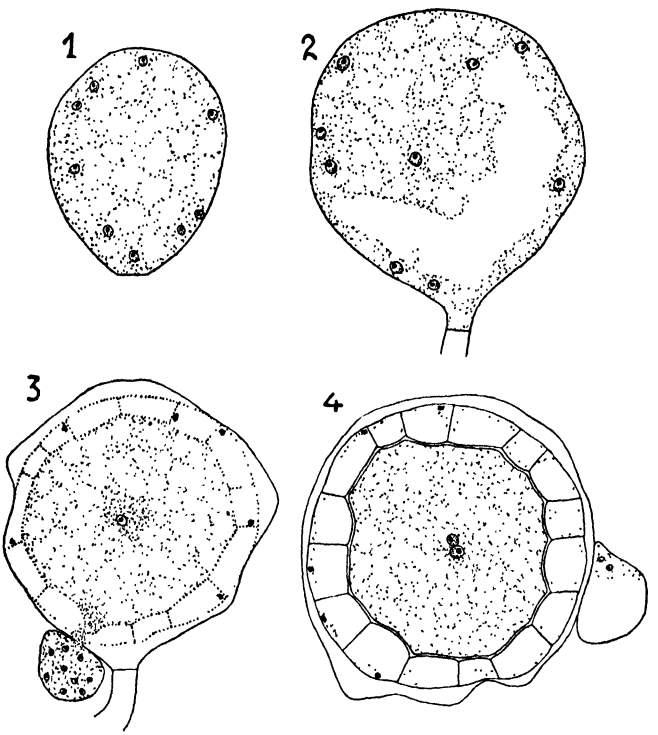


FIG. 43.—*Araiospora pulchra*. Development of oogonia. 1. Young oogonium with peripheral nuclei. 2. Fundament of central egg cell. 3. Mature egg cell whose copulation papilla is in contact with the antheridium. 4. Young oospore with peripheral, faveolate cells. (× 860; *after King*, 1904.)

gium, and the swollen portion forms a tube into which the swarm spores migrate (Fig. 41, 2) and from which they are liberated. This species possesses antheridia and oogonia whose development is still unknown.

Araiospora is similar in structure and mode of life. It differs from *Rhiphidium* by the presence of two kinds of sporangia, simple and echinate types (Fig. 42). The latter possess a solid membrane and may pass through a resting period; they are formed under unfavorable growth conditions, such as poor nutrition, low temperature and in places where,

on account of their surroundings, zoospore emission cannot take place, such as in aerial mycelium in gelatin cultures (Minden, 1916). Apparently they have a biological significance similar to that of gemmae: they germinate like ordinary sporangia.

King (1904) investigated the cytological development of *A. pulchra*. As in the Saprolegniaceae, zoospores arise by cleavage. At the time the oogonium is cut off, its protoplasm forms a homogeneous network with 35 to 50 nuclei, but whether this large number is caused by division is still unknown. They migrate to the periphery, thus causing a vacuolation of the interior of the oogonium (Fig. 43, 1). Thereupon most of the protoplasm migrates back to the middle without the nuclei, causing large vacuoles at the edge. The central mass of protoplasm becomes the egg (Fig. 43, 2). In the middle is differentiated a reticulate, strongly staining mass of protoplasm which apparently corresponds to the coenocentrum of the Peronosporeae. Meanwhile the nuclei at the edge have divided once. One of them migrates back into the egg and lies in the neighborhood of the coenocentrum (Fig. 43, 3); the others remain in the peripheral layer of protoplasm, the periplasm.

In the antheridium also, the nuclei divide. Only one of them is functional and at fertilization passes over into the oogonium. Individual peculiarities, such as the absence of a conjugation tube and the formation of a receptive spot, are reminiscent of the Peronosporaceae. The egg surrounds itself with a thick wall and becomes an oospore (Fig. 43, 4). The fusion of the two nuclei takes place only at germination. The periplasm changes into a peculiar faveolate sheath. The further fate and germination of the oospore is unknown.

Peronosporaceae.—A few primitive forms are saprophytic on earth or fresh water; the higher ones are exclusively parasitic on land plants.

The mycelium is ramose and consists of hyaline, generally comparatively thick hyphae which are coenocytic when young or when well nourished, but which become septate in age. In some species of *Pythium* and *Phytophthora*, they may unite into growths apparently adapted to resist to external influences (Fig. 44, 1). Several species form thick-walled gemmae. In saprophytic forms, the mycelium is both intra- and extramatrical and in the latter case forms (particularly in water) Saprolegniaceous clumps; in the other cases, there is no differentiation into extramatrical hyphae and rhizoids. The parasitic forms develop exclusively within the substrate and only liberate conidiophores. In the simple representatives of this group, as in *Pythium* and *Phytophthora*, the mycelium is both intercellular and intracellular and generally forms no special haustoria penetrating the host. In the other genera it is exclusively intercellular and penetrates the host cells by characteristic haustoria, which in *Albugo*, *Plasmopara*, *Bremia*, etc., are like short sacs and in some species of *Peronospora* branch digitately and occasion-

ally fill up the whole host cell like a knot. Biologically, from the simpler to the higher forms, there is an increased adaptation to parasitism. *Pythium* and *Phytophthora* kill the infected tissue, *Albugo* and *Peronospora* only stimulate it to hypertrophy or to storage of food. Some species of both these genera winter over in the rhizomes of the host and penetrate the whole shoot. Some species of *Peronospora* in flowers seem to grow up the stem as intercellular parasites and only develop their conidiophores on the corolla. Furthermore, most species of *Pythium* and *Phytophthora* are plurivorous and may be cultivated on artificial media; *Albugo* and *Peronospora* are much more specialized and will not grow saprophytically.

Asexual reproduction takes place by sporangia which, even in the most highly metamorphosed form, are cut off as multinucleate structures

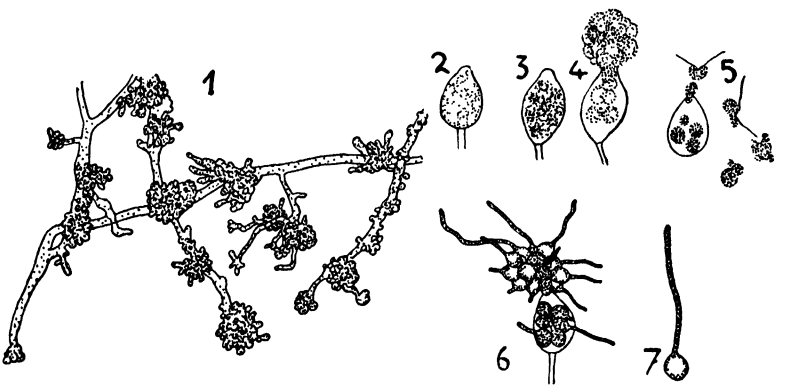


FIG. 44.—*Phytophthora Syringae*. 1. Mycelium. *Phytophthora Arecae* 2 to 7. Germination of zoosporangia. (× 215; *after Rosenbaum*, 1917.)

at the ends of hyphae or hyphal branches; nuclear divisions do not occur in them as in members of the Saprolegniaceae (Ruhland, 1904, disputed by Istvanffi and Palinkas, 1913). Within the family they undergo notable changes which were first recognized by Bary (1863). There are three stages of development corresponding to the tribes Pythieae, Albugineae and Peronosporeae.

Pythieae.—In this tribe *Pythium* and *Phytophthora* take the lowest position. In the simpler species of *Pythium* (Subgenus *Aphragmium*), true zoosporangia do not occur. Occasional hyphae emit their protoplasm into a germ sac (remains of a first swarm stage with terminal flagella) where it changes to zoospores without being abjointed from the rest of the mycelium (Fig. 45, 2 to 5). For this lower degree of development, it is further characteristic (as in the holocarpic Chytridiaceae) that, in proportion to their thallus, they can produce a very large number of spores; *e.g.*, in *Pythium gracile*, almost the whole content of the hypha

is discharged as zoospores. Most of the forms belonging here are aquatic. *Pythium Indigoferae*, rarely forms zoospores and reproduces almost exclusively by oospores, wasteful of material.

In the subgenus *Nematosporangium*, the sporangia are filamentous, but separated from the rest of the mycelium by a septum. In the sub-

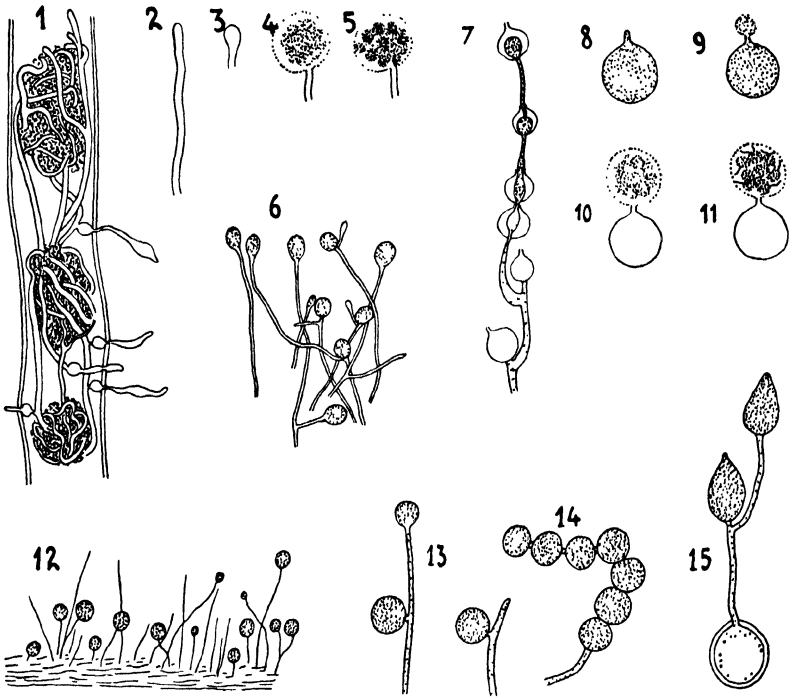


FIG. 45.—*Pythium*. Forms of sporangium. *Pythium gracile*. 1. Filament of *Vaucheria* with parasite. 2, 3. Vegetative hyphae which have swollen terminally. 4. The protoplasm has passed into a germ sac. 5. Zoospore formation. *Pythium proliferum*. 6. Zoosporangia. 7. Proliferating zoosporangiferous hyphae. 8 to 11. Germination of zoosporangia. *Pythium diacarpum*. 12. Habit of fungus on decaying wood. *Pythium intermedium*. 13, 14. Formation of zoosporangia. *Pythium palmivorum*. 15. Germinating oospores. (1 × 565; 2 to 5 × 330; 6, 12 × 67; 7 × 100 8 to 11, 13, 14 × 200; 15 × 270; *after Butler*, 1907.)

genus *Sphaerosporangium*, the characteristic spherical sporangia lead to true conidia; in the section *Orthosporangium*, *e.g.*, *P. proliferum*, they always remain attached to the mycelium and germinate *in situ* (Fig. 45, 6 and 7); here they behave as ordinary sporangia. In the section *Metasporangium*, *e.g.*, *P. debaryanum* and *P. intermedium* (Fig. 45, 13 and 14), they may fall off and be disseminated by wind or water as true conidia. In their manner of renewal, also, these two sections may be distinguished.

In *P. proliferum* the sporangia are, as in many Saprolegniaceae, renewed by proliferation, which may be repeated until almost all the protoplasm has been used up in the formation of zoospores (Fig. 45, 7). In the conidia formation of *P. intermedium*, the sporiferous hypha continues in its growth under the terminal conidium, pushes it aside and terminally cuts off a new conidium: this process may be repeated, resulting in racemose groups of conidia (Fig. 45, 13). Also the conidia may be cut off successively in moniliform chains (Fig. 45, 14).

In *Phytophthora*, only conidial forms are known. These conidia are renewed like those of *Pythium*. There is cut off terminally on each of the extramatrical hyphae, a conidium which is pushed aside by the developing hyphae, and falls off, as described for *Pythium intermedium* (Fig. 45, 13).

In the higher Peronosporaceae, differentiation has extended to the sporiferous hyphae. Just as the sporangia, which are firmly attached to the mycelia and hardly to be distinguished from them, result in morphologically and biologically differentiated conidia which break loose from the mother plant and fulfil a new function—that of dissemination—their sporiferous hyphae develop to differentiated conidiophores. The extramatrical hyphae no longer cut off conidia and when brought to any nutritive substrate, themselves develop to mycelia, but they represent characteristically formed sporophores which perform this function exclusively. They no longer develop indefinitely as typical hyphae, but limit their growth and only when the conidiophore is mature, does the terminal abstriction of conidia occur. Because this limited growth permits only one conidium to be cut off from a hypha, only those forms have been retained in which this loss is compensated by other adaptations. In this respect, two types are known, that of the Albugineae and that of the Peronosporeae.

Albugineae.—The sporiferous hyphae of *Albugo*, as those of the Pythieae, are simple. They differ from them in the limitation of growth, in their thicker membrane at the base (Fig. 46, 5) and in the peculiarity that several conidia are cut off at a hyphal tip in basipetal sequence, as in *Pythium intermedium*. From the hyphae which grow luxuriantly through a substrate, a few nuclei enter the young sporiferous hypha and, surrounded by thick protoplasm, migrate to the tip. When five to seven nuclei have collected, the tip is abjointed and rounds off as a conidium. The septum is laid down as a ring from the hyphal wall to the middle (Fig. 46, 1 and 2); it is differentiated subsequently into three layers, two outer, deeply staining with haematoxylin, and a central one which takes up a small amount of dye (Fig. 46, 3 and 4). After the conidium has rounded off, the original hyphal wall dissolves at the constriction; a conidium and hypha are only connected by the plate. The distal outer layer of the plate is let into the conidial wall, the proximal outer layer

into the hyphal wall. The middle layer elongates, thus becoming narrower and is finally dissolved, serving as a disjunctor. Meanwhile new nuclei have entered the sporiferous hypha and are used in the formation of another conidium. Apparently, nuclear divisions do not occur in conidiophores and conidia.

Peronosporeae.—Here only one conidium arises at each hyphal tip; between it and the hypha, there is formed a single short sterigma of a water-soluble substance which facilitates the abscission (Rostowzew, 1903). The disadvantage of this single abscission is compensated in various forms in a definite manner; thus the conidiophores of *Basidiophora* are still unbranched, as in *Albugo;* at their tips they are slightly

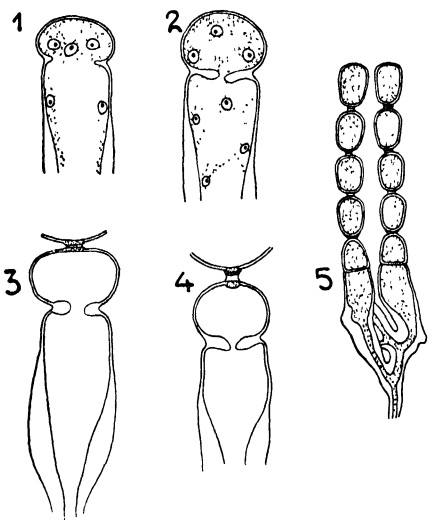


FIG. 46.—*Albugo candida.* 1 to 4. Formation of conidia. *Albugo Portulacae.* 5. Catenulate conidia. (1 to 4 × 900; *after Bary and Rosen.*)

clavate and closely covered with numerous small processes, each of which cuts off a conidium (Fig. 47, *a*); in this manner, there arises on a single conidiophore a large number of spores. Also in *Bremia* the tips of the branches are swollen and covered with short processes. In the other genera there appears a tendency to repeated branching. In some species of *Plasmopara* (Fig. 48, *A*) and in part in *Sclerospora*, there is present a typical monopodial principal axis from which radiate shorter, often trichotomous branches. In most species of *Peronospora* the conidiophores form regular trees with a high trunk and a definitely differentiated crown whose branches are forked dichotomously up to twelve times. How effective this forking of the conidiophores is may be seen from a calculation of Weston, where for *S. philippinensis* the

number of conidia formed per square centimeter of infected leaf surface is about three million.

In contrast to variability of the conidiophores, the conidia appear approximately the same. They are spherical, ellipsoidal or ovoid, hyaline with a smooth, hyaline, brownish or dirty violet membrane. In most genera a short germ papilla is present at the top. Under certain conditions, the conidia of *Pythium* may thicken their wall and remain

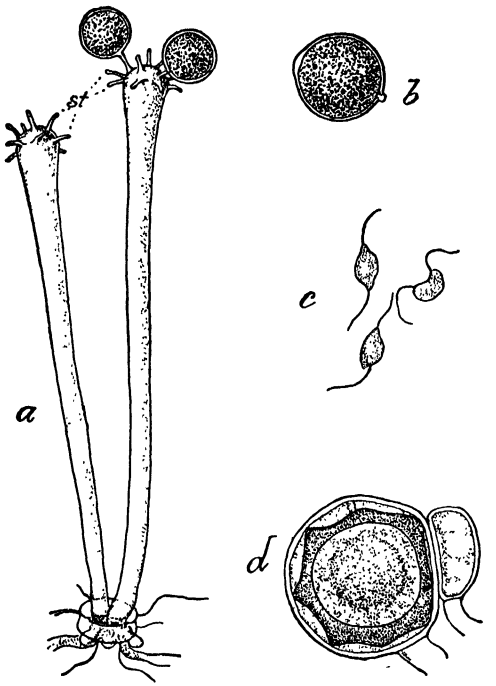


FIG. 47.—*Basidiophora entospora*. *a*, two conidiophores emerging from a stoma; *st*, short sterigma which forms a conidium; *b*, conidium with apical papilla and remains of stalk; *c*, zoospore from germinating conidium; *d*, cogonium with mature oospore, whose exospore is ridged. Empty antheridium at the right. (*a* × 230; *b* × 540; *c*, *d* × 550; *after Roze and Cornu.*)

capable of germination up to 11 months. In some species of *Albugo*, the wall is thickened equatorially, forming a ring (annulus). Furthermore, in *Albugo* the first conidium of a chain is generally larger than the others and has a membrane of even thickness. When such a conidiophore, by raising the epidermis from the tissue, breaks out of the host and the spore chains break up, these first conidia remain clinging to the epidermis of the host. Possibly these serve exclusively to raise the epidermis and are not capable of germination. Therefore they are called "buffer cells."

The conidia and sporangia of the Peronosporaceae behave very differently on germination. In *Pythiomorpha gonapodioides* the zoospores are formed in the zoosporangium and are discharged by the solution of the papilla and the rupture of the inner membrane. They come to rest, encyst, and germinate either by hyphae or swarming. The second swarm stage is non-motile. Secondary sporangia are sometimes formed by proliferation of the primary sporangia as in *Saprolegnia* (Kanouse, 1925). In *Pythiogeton* at the evacuation of the sporangium the whole content passes out into a sac in 20 to 60 seconds (Fig. 49, 1);

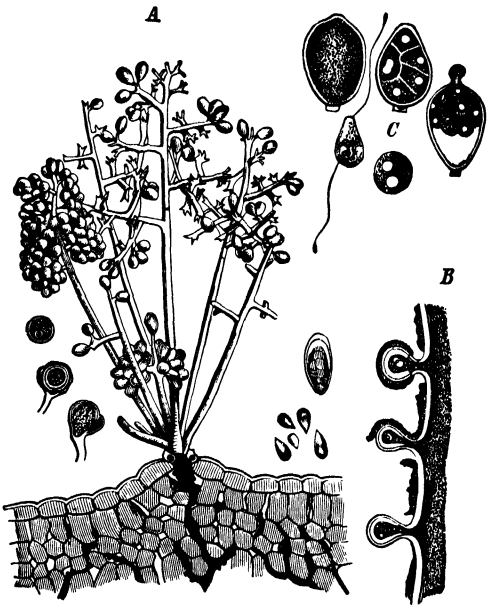


FIG. 48.—*Plasmopara viticola*. *A*, conidiophores with oogonia and oospores at the left; *B*, haustoria; *C*, germinating conidia. (*After Millardet.*)

this ruptures and discharges the naked masses of protoplasm as illustrated (Fig. 49, 2). Shortly there appear indentations which penetrate deeper so that after 15 to 20 minutes the outlines of the zoospores are visible (Fig. 49, 3). These round off and swim away. Also in *Pythium*, the sporangia or conidia discharge their undivided contents into a sac where it then falls apart into swarm spores which are liberated by the bursting of the sac (Fig. 44, 4 and 5, 9 to 11). Under certain conditions *P. debaryanum* may germinate by a germ tube. In *P. ultimum* zoospore formation is entirely suppressed and only tube germination is known. After *Pythium*, the process of germination becomes continually simpler; thus in *Pythiomorpha* the zoospores are formed already in the sporangium.

In *Phytophthora* (Fig. 45, 2 to 7), *Albugo, Basidiophora, Sclerospora* and, in part, *Plasmopora* (Fig. 48, *C*), the stage of the germ sac has almost entirely disappeared. Here the mature zoospores swarm directly out of the conidium. In other forms, the formation of swarm spores is suppressed and replaced by the direct development of conidia to a mycelium. Thus in *Plasmopara pygmaea,* the undivided content of the conidium swells out of the top, rounds off and puts out a germ tube. In *Bremia,* the conidium germinates directly by a germ tube which has grown out of a papilla at the tip; in *Peronospora* the papilla is lacking and the germ tubes come from any portion of the conidium.

Wherever zoospores are formed in the Peronosporaceae they are reniform and possess two lateral flagella (Fig. 49, 4; 44, 5); thus they are

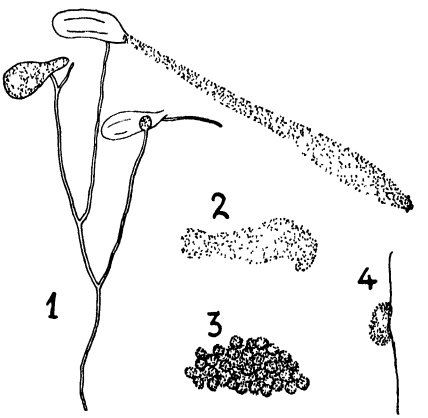


FIG. 49.—*Pythiogeton transversum.* 1. Hyphae with three zoosporangia, one of which is discharging. 2. Protoplast has formed an elongate mass on emerging. 3. Zoospore formation. 4. Single swarming zoospore. (*After Minden,* 1916.)

connected directly to the Saprolegnieae of the *Achlya* type. Those of *Pythiogeton* swim about for a while (up to two days) then come to rest, surround themselves with a membrane and germinate to a mycelium. Butler (1907) has observed in *Pythium diacarpum* and Murphy (1922) in *Phytophthora infestans* the shedding of the membrane, as in *Dictyuchus;* the zoospores which have found no suitable substrate come to rest and surround themselves with a membrane. After a certain time they again slip out with the same reniform appearance and swarm further. The phenomenon has further been described by Bary for *Pythium proliferum* and by Atkinson for *P. intermedium;* ocasionally the biflagellate zoospores may split into two uniflagellate ones; this appears to be only a morbid specimen, however, since Butler could not find in his material the process described by Atkinson.

In addition to this asexual reproduction, sexual organs, antheridia and oogonia are known in most of the Peronosporaceae. With the

exception of *Pythium*, they arise only in the tissue of the host as clavate, terminal or intercalary cells of hyphae or hyphal branches; their development shows ascending differentiation proceeding parallel to the lines of development of conidiophores and conidia.

In *Pythium* 10 to 15 nuclei enter the young oogonium, and three to six the young antheridium; thereupon the swelling is abjointed from the rest of the hypha. About simultaneously in both organs, the nuclei undergo division (Fig. 50, 2), in which there have been counted in *P. ultimum* (Trow, 1901) at least six chromosomes and in *P. debaryanum* (Miyake, 1901) approximately eight. Meanwhile the protoplasm of the oogonium has been differentiated more or less definitely into a thicker, denser, central ooplasm and spongy periplasm. In *P. ultimum*, all nuclei

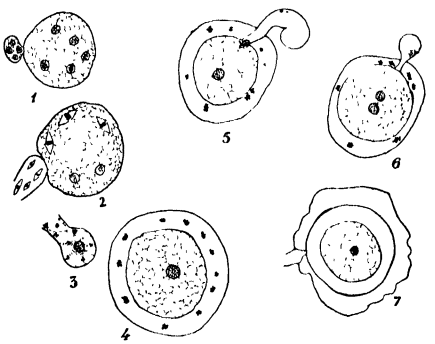


FIG. 50.—*Pythium debaryanum*. Gametangial copulation. 1. Young oogonium and antheridium. 2. Mitoses. 3. Degeneration of all but one male nuclei. 4. All but one female nuclei migrate to the periphery and degenerate. 5, 6. Plasmogamy. 7. Mature oospore. (*After Miyake*, 1901.)

but one migrate to the periplasm and degenerate there. In *P. debaryanum*, all migrate into the periplasm, then one returns while the others degenerate (Fig. 50, 4). Meanwhile in the antheridium, at least in *P. debaryanum*, all nuclei but one disintegrate (Fig. 50, 3); in *P. ultimum* they all appear to remain intact. The antheridium puts forth a conjugation tube into the oogonium and allows the male nucleus (in *P. ultimum* one of the many), together with a part of the male protoplasm, to pass over into the egg cell; there it lies in the vicinity of the female nucleus but only fuses with it after a long time. Shortly after nuclear migration, the central ooplasm of the oosphere surrounds itself with a membrane, during which the greater part of the periplasm is resorbed; later a thick-walled endospore is formed on its inner side; but a true epispore, laid down by the periplasm, is not present. In both species the oospore germinates by a germ tube which develops to a hypha. In *P. ultimum* it can take place after 24 hours. In other species of *Pythium* different germination forms have been described, as in *P. vexans*, zoospore

germination and in *P. proliferum* and *P. palmivorum*, germination with a hypha which ends in a sporangium (Fig. 45, 15).

In *Phytophthora* two groups may be distinguished in the structure of the sexual organs. The *P. cactorum* group, including *P. Nicotianae*, agrees entirely with *Pythium debaryanum, i.e.*, an antheridium is placed at the side of an oogonium into which it forces a fertilization tube. These forms are called **paragynous.** The *P. infestans* group, including *P. erythroseptica, P. Phaseoli, P. parasitica* and *P. Arecae*, shows a new structure, unique in the oomycetes; in it the oogonium grows through the antheridium so that the latter sits like a collar on the oogonial stipe. These forms are called **amphigynous.** Both types, however, are not so fundamentally different that they may be separated generically; thus in *P. Syringae* and *P. Fagi* occasionally amphigynous antheridia appear among the paragynous (Himmelbaur, 1911; Lafferty and Pethybridge, 1922).

The life cycle may be discussed for a representative of the amphigynous group, *P. erythroseptica* (Pethybridge, 1913; Murphy, 1918). Its antheridium always arises earlier than its oogonium, and generally as a lateral outgrowth of a hypha from which later, as the material is used up, they are abjointed. In youth they contain 8 to 10 nuclei. Although the species is homothallic the oogonia arise on another hyphal branch and generally laterally. When an oogonium fundament comes in contact with an antheridium, in a short time, probably within a few hours, it grows through it. The fundaments which find no antheridia, cease their growth, except in *P. infestans* which develops parthenogenetically (Pethybridge and Murphy, 1913). Outside the antheridium, the oogonial fundament swells up to an oogonium (Fig. 51, 6). The strong stream of protoplasm flows out of the sporiferous hyphae into the oogonium until the hypha is almost empty; thus during this time the oogonium contains 90 to 100 nuclei. Generally it is not separated from the sporiferous hypha by a wall; but later the connecting passage is closed by a plug of highly refractive material.

Two-thirds of the nuclei degenerate both in oogonia and antheridia. Thereupon they arrange themselves peripherally, with one in the center of the oogonium and undergo a single simultaneous division. All peripheral nuclei and one daughter of the central nucleus degenerate (Fig. 51, 7). Meanwhile there has collected around the central nucleus the somewhat denser ooplasm, while the periplasm remains almost structureless. It is entirely resorbed by the ooplasm, so that shortly after fertilization only the remains of the degenerated nuclei are present. Meanwhile in the antheridium the nuclei have also undergone division and all but one disintegrate. Then the oogonial wall is dissolved gradually in one spot (receptive spot). Because of its higher osmotic pressure, the antheridium pushes a short fertilization tube into the oogonium (Fig.

51, 7, lower left) and allows its nucleus with most of the protoplasm to pass over. Fusion of the two nuclei takes place very late during the maturation of the oospore. The wall of the mature oospore consists of three layers, the original membrane, a thin hyaline primary endospore and a thick secondary endospore which consists of reserve material which is dissolved at germination. This takes place through a hypha

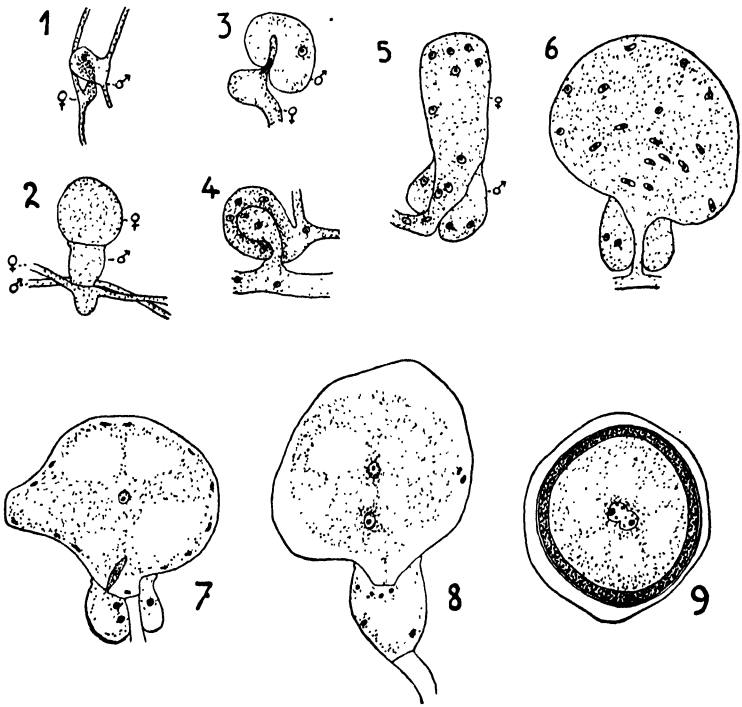


FIG. 51.—*Phytophthora erythroseptica.* Development of oospores. 1. Oogonium beginning to penetrate antheridium. 2. 2 hr. 20 min. later, the oogonium begins to swell beyond the antheridium. 3. Same as 1. 4. Older stage. 5, 6. Development of oogonium after it has grown through the antheridium. 7, 8. Fertilization. 9. Immature oospore. (1, 2 × 420; 3 to 9 × 800; *after Pethybridge,* 1913, *and Murphy,* 1918.)

which, according to circumstances, may develop to a mycelium or cut off a conidium.

The species of the Peronosporeae, *e.g.*, *Plasmopara alpina* (Rosenberg, 1903), *P. densa, Sclerospora graminicola, Peronospora vernalis* (Ruhland, 1904), *P. Alsinearum, P. effusa* (Berlese, 1898), *P. Ficariae* (Berlese, 1898; Kruger, 1910) and *P. parasitica* (Wager, 1900; Kruger 1910) show essentially the same steps in development as *Phytophthora erythroseptica;* only their antheridia are paragynous and at the time of fertilization contain all the nuclei of which only one enters the oogonium. In regard

to protoplasm and the length of life, however, their oogonia show a continuous development, due to retardation of the degeneration of the superfluous nuclei in the periplasm. While in the Saprolegniacae and in *Phytophthora* this begins before mitosis (*i.e.*, before the gametangial nuclei are activated as sexual nuclei) and continues after it; in the Peronosporeae and in the Albugineae, as far as is known, it begins after mitosis; thus at fertilization the superfluous nuclei are still intact and, in conjunction with the periplasm, are adapted to creative activity. The transition from *Phytophthora* takes place gradually; thus in *Plasmopara* and *Sclerospora* the periplasm, as in *Phytophthora*, has only a slight structure and even during mitosis is not sharply separated from the ooplasm. Especially in the last named genus the periplasm is always in several layers around the oogonial wall which persists and surrounds the oospore for a considerable time. In some species of *Peronospora* it behaves similarly; in others it increases in importance and becomes much denser and more homogeneous than the ooplasm; instead of the oogonial wall becoming strengthened, however, it deposits on the oospore itself a strong epispore with verrucose or reticulate sculptures; thus the oogonial wall remains thin and transitory and collapses after spore maturity. Only here the oospores have become true independent resting spores. Furthermore, in *Peronospora* there collects in the center of the oosphere, a deeply staining dense mass of protoplasm (the coenocentrum) in the vicinity of which the female nucleus is placed; this will be discussed in detail under the Albugineae.

The germination of the oospores in *Plasmopara* takes place through zoospores, in *P. viticola* under certain conditions also with a germ tube ending in a large conidium (Ravaz and Verge, 1913), in *Sclerospora* and *Peronospora* through a germ tube which develops in the host to a mycelium.

Opinions differ regarding the position of meiosis in each of these three genera. According to Wager, Rosenberg and Ruhland it takes place just before fertilization; according to Krüger it takes place just after fertilization in the first division of the zygote nucleus. In rare cases (*e.g.*, *Peronospora Ficariae*) it is connected directly with nuclear fusion, but ordinarily takes place much later in the germination in the oospores. According to present conceptions, and according to what is known concerning change of nuclear phase in other fungi, Krüger's theory might easily be the correct one. In any case, further investigation of the question would be desirable.

The Albugineae, because of their special position in regard to conidiophores and fertilization, afford unique types, which are the most primitive known in the Peronosporaceae. They are further noteworthy in that in the same genus (*Albugo*) they go through fundamental changes while the form of the conidiphore remains entirely constant.

In their youngest fundaments, the antheridia and oogonia agree with those of other Peronosporaceæ. They arise as terminal swellings of hyphal branches, whereby the antheridia acquire about 35 nuclei, the oogonia up to 300. At the spot where the antheridium is attached to the oogonium, the oogonial and antheridial walls are digested by an enzyme; as possibly the osmotic pressure of the oogonium is higher than that of the antheridium, the oogonial content, surrounded by a membrane, bulges like a papilla into the antheridium. This papilla is unfortunately named a receptive papilla. Later this is turned back and is followed by the fertilization tube which penetrates the pore.

In the oogonia the nuclei are regularly scattered throughout the protoplasm. During their simultaneous division a fundamental

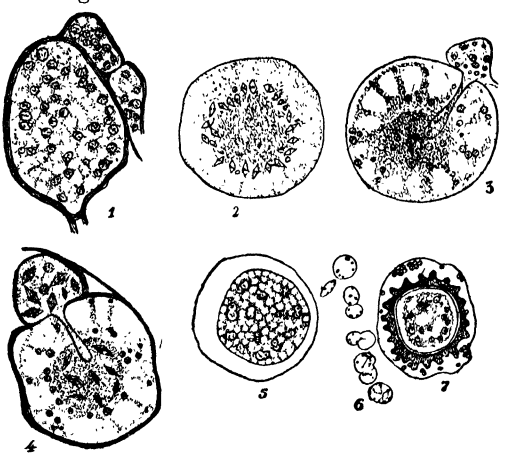


FIG. 52.—*Albugo Bliti*. Development of oospores. 1. Antheridium and oogonium. 2. Mitoses at the periphery of oosphere. 3, 4. Penetration of copulation tube. 5, 6. Copulation figures of male and female nuclei. 7. Mature oospore. (*After Stevens*, 1899.)

rearrangement occurs in the whole oogonium. Most of the protoplasm draws together into the dense oosphere, while the periplasm remains spongy and much vacuolate; then the nuclei are extruded from the oosphere and deposited in the periplasm.

The details of development in the various species of *Albugo* differ considerably from each other. In *Albugo Bliti* (Stevens, 1899) and *A. Portulacæ* (Stevens, 1901), a marked border layer*ae* forms between the periplasm and oosphere. A part of the nuclear spindles are so placed (Fig. 52, 2) that only one daughter nucleus lies in the periplasm the other in the oosphere; in this manner 40 to 50 nuclei return to the oosphere. Here they soon divide for a second time (Fig. 52, 4), while those of the periplasm remain resting. Meanwhile the protoplasm in the center of the oosphere has become condensed into a small deeply staining coenocentrum, which appears to attract the nucleus. Its signifi-

cance is still obscure; possibly it is the dynamic center of the polyenergid egg or an organ of nourishment for the nucleus.

In the antheridium also the nuclei go through two mitoses (Fig. 52, 4); the conjugation tube penetrates to the vicinity of the coenocentrum, dissolves at the tip and about 100 nuclei enter the egg; they approach the female nuclei and slowly fuse with them (Fig. 52, 5 and 6). Hereupon the fertilization tube and the coenocentrum are dissolved, the egg is surrounded with an exospore near which a primary and a secondary endospore are laid down.

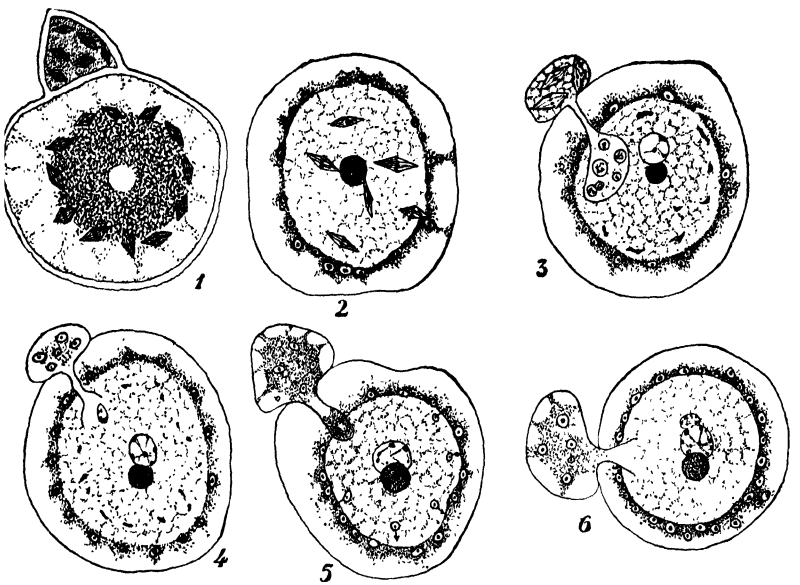


FIG. 53.—*Albugo Tragopogonis*. 1. Antheridium and oogonium with mitoses. 2. Nuclei near the coenocentrum dividing while the peripherial nuclei of the egg degenerate. 3. The rest of the egg nuclei except one, degenerating. 4. A male nucleus enters as the female approaches the coenocentrum. *Albugo candida*. 5. Penetration of copulation tube. One nucleus remains in egg cell while the others migrate to the periplasm. 6. Fusion of male and female nuclei. (*After Stevens*, 1901.)

Two species, *A. Tragopogonis* (Stevens, 1901) and *A. Ipomoeae-Panduranae* (Stevens, 1904), correspond, as far as the maturation of the coenocytic egg, with *A. Bliti*. Of the 100 potential sexual nuclei only one is functional; it lies next the coenocentrum, develops to four times its original size when in *A. Tragopogonis*, the other nuclei dissolve (Fig. 53, 3 and 4) or, in *A. Ipomoeae-Panduranae*, migrate to the periplasm. From the equally multinucleate antheridium, one or more nuclei enter the egg (Fig. 53, 4); one of them fuses with the female nucleus while the others are dissolved. The diploid nucleus soon divides repeatedly so that the oospore winters over with 30 to 40 nuclei.

In still other species, as *A. candida* (Davis, 1900; Stevens, 1901; Krüger, 1910) and *A. Lepigoni* (Ruhland, 1904), reduction has proceeded a step further. Here already at the differentiation of the protoplasm, a nucleus remains behind in the egg cell (Fig. 53, 5) and then divides, at least in *A. candida*, simultaneously with that of the periplasm. One daughter nucleus becomes an egg nucleus, the other degenerates. Ooplasm and periplasm are no longer so distinct as in *A. Bliti*; although the coënocentrum is much more highly developed and has become a sharply defined granular mass, rich in food, which can attain fourfold the cross-section of the nucleus; frequently it is also surrounded by a halo of less deeply staining, radial protoplasm. As in the other species of *Albugo* with only one functional egg nucleus, here also the zygote nucleus divides repeatedly after fertilization, so that the oospore winters over with a large number of nuclei. Except for this peculiarity and the formation of the coenocentrum, the Albuginaceae in A. *candida* have attained the stage of *Phytophthora*.

As far as is known, in all species, at germination, the oospores swell until the exospore bursts; the content of the endospore bulges out like a sac, bursts and liberates the biflagellate zoospores.

If the developmental forms of the gametangia of the Peronosporaceae are compared with those of the Leptomitaceae, there appears a continuation of the tendency to limit fertilization to only a certain number of nuclei, *i.e.*, to favor some nuclei as sexual nuclei. Thereby, the female gametangia from selection become more strongly developed than the male; as in *Araiospora* of the Leptomitaceae, the number of functional nuclei falls to one. In the male gametangia, however, again like the Saprolegniaceae all nuclei remain equivalent; as many of them are used as there are present functional nuclei in the corresponding female gametangia.

The female gametangia of the Peronosporaceae develop still further. While in the Saprolegniaceae there is a certain natural selection of the (virtual) female gametes, since only a part of the nuclei is used in egg formation, in the Peronosporaceae this differentiation between functional and supernumerary parts extends to the protoplasm and divides it into the gonoplasm (which takes part in egg formation) and periplasm (which has only vegetative duties). This distinction must have arisen so that differentiation ceases after the energids (as in *Albugo Bliti*) have been differentiated into functional and supernumerary. Thus a differentiation does not extend to the individualization of single functional energids, as in the Saprolegniaceae, but it leaves these unchanged in the center of the female gametangium in the form of a multinucleate egg. For this reason the coënocytic egg of the Peronosporaceae does not correspond to a single egg of the Saprolegniaceae but to the majority of eggs contained in an oogonium, just as an egg of the Saprolegniaceae corresponds to several gametes of *Olpidium*. Caryologically, the difference is not

very significant, as all functional nuclei are fertilized by male nuclei; only as it is a question of a simultaneous process in the same organ, this multiple fertilization, in contrast to the Saprolegniaceae, is consummated by a single sexual act.

Selection goes still further and removes all but one nucleus from the coenocytic egg into the periplasm. Thus in every oogonium a single uninucleate egg is formed secondarily; this should not be considered homologous to a true gamete as its phylogeny shows it to be a coenogamete which has become uninucleate. Thus in the highest Oomycetes, the number of functional female energids sometimes is reduced to one. Similarly also in the antheridia of some, only one nucleus is functional and all the others degenerate. Thus between the contents of two gametangia only one sexual act and one fertilization occurs and its product is only a single uninucleate zygote, which in *Olpidium* was the product of two daughter cells of the gametangium but is here the product of two gametangia themselves: as in the development of the zoosporangium to conidium, here the whole organ has assumed the function of a part.

The Pythieae form the transition from the Leptomitaceae and are marked by the possession of true zoosporangia. Four genera should be mentioned here, *Pythium*, *Phytophthora*, *Pythiomorpha* and *Pythiogeton*. *Pythium*, as has already been indicated on page 75, is divided into three subgenera according to the structure of their sporangia: *Aphragmium*, *Nematosporangium* and *Sphaerosporangium*. To *Aphragmium* belong *P. gracile* which has been found in the north temperate zone, parasitic on Chlorophyceae and saprophytic in soil, and *P. Indigoferae* which in British India is epiphytic (?) on leaves of *Indigofera arrecta*. To *Nematosporangium* belong *P. monospermum* which appears in water on decaying insects and *Lepidium* seedlings, and *P. aphanidermatum* which in the United States is parasitic on sugar-beet seedlings, in Hawaii on sugar cane and in India on ginger, tobacco and *Papaya*. The subgenus *Sphaerosporangium* finally is divided into two sections; *Orthosporangium*, in which the sporangia remain attached to the mycelium; and *Metasporangium*, in which the conidia fall off. The species of *Orthosporangium* are mostly aquatic on plant and animal remains and renew their sporangia by proliferation as *P. proliferum* and *P. diacarpum*. The species of *Metasporangium* have passed over to terrestrial habitats and renew their conidia by lateral sprouting of sporiferous hyphae, as *P. debaryanum* which causes the destruction of young seedlings of crucifers, sugar beets, etc., *P. palmivorum* which in India causes a heart rot of coconuts, and *P. intermedium* which in Europe and North America is saprophytic on garden soil and parasitic on fern prothallia.

These forms are so closely allied to *Phytophthora* that a border line may not be drawn. In some of its species the conidiophores do not possess an entirely mycelial character, as *Phytophthora erythroseptica*

in which they do not project above the substrate but cut off conidia under water (Pethybridge, 1914). Also as regards the germination of conidia, transitions are very gradual; thus *P. Arecae* germinates generally with a sac as *Pythium palmivorum* (Rosenbaum, 1917). In contrast to *Pythium*, however, all species of *Phytophthora* so far known are parasitic. *P. infestans* causes the late blight of potatoes; it goes over to various other Solanaceae and Scrophulariaceae; in damp earth, the conidia remain capable of germination up to 4 weeks (Murphy, 1922.) *P. erythroseptica* causes a similar disease of potatoes in which the infected tissue of the tubers becomes salmon color after a half-hour and in a few hours assumes a deep purple brown color. The group of *P. omnivora* occurs in several strains, rather obscure in choice of host but morphologically distinct in pure culture, which have earlier been given special names, as *P. Syringae*, *P. Cactorum* and *P. Fagi* (Himmelbaur, 1911). It appears on all kinds of hosts and causes particularly rots, in cacti, pear, buds of lilac, beech seedlings, etc. *P. Faberi* causes a bast rot of cacao, *Hevea*, etc., *P. Phaesoli*, an abscission of the pods of *Phaseolus lunatus*, and *Phytophthora Arecae* a heart rot of *Areca* palms.

Both *Pythiomorpha gonapodioides* and *Pythiogeton utriforme* have been found exclusively on rotting fruits and other plant parts in water.

The Albugineae are characterized by short sterigma-like conidiophores which cut off successively chains of conidia; they are generally laid down in a thick sorus under the epidermis of the host and are liberated by its rupture. Up to the present only one parasitic genus is known, *Albugo*, whose species cause hypertrophies and malformations; thus *A. candida* on crucifers (Melhus, 1911), *A. Tragopogonis* on composites, *A. Ipomoae-Panduranae* on sweet potatoes *A. Bliti* on Amarantaceae and *A. Portulacæ* on *Portulaca*.

The Peronosporeae, finally, are distinguished by the development of the sporiferous hyphae into true conidiophores; this takes place so gradually that systematic classification, which here rests only on the sporiferous hyphae, can only be certain of the most marked types and must rely on subjective measurements on many transitional forms (Wilson, 1914). The only species of *Basidiophora*, *B. entospora*, lives on leaves of composites. Some species of *Sclerospora* are dreaded in India, the Dutch East Indies and the Philippines, as a cause of leaf disease of maize. Another species, *S. graminicola*, appears on various grasses in Europe and North America. *Plasmopara* is economically important as a cause of plant disease. Its conidiophores and conidia vary markedly in form and size from one host genus to another and sometimes even in the same genus (Wartenweiler 1918). In *P. nivea* and *P. viticola*, the downy mildew of grapes, the conidia germinate generally with zoospores; in *P. pygmaea*, on various Ranunculaceae, in *P. alpina* on *Thalictrum alpinum* and *P. densa* on Scrophulariaceae, generally with

germ tubes, whereby their contents pass out of the papilla as a ball. *Bremia Lactucæ* causes a rot of various composites, especially lettuce and artichokes. It is divided into several biological forms which may be partially separated biometrically (J. Schweizer, 1919). *Peronospora* is divided into a large number of smaller morphological and biological species, which are usually specialized on single host genera and often on single host species (Gäumann, 1918*a*, 1923). *P. cannabina* causes a disease of hemp, *P. Brassicae* of cabbage, *P. Schleideni* of onions, *P. Schachtii* of sugar beets, *P. Spinaciae* of spinach.

Having reached the end of the Oomycetes we will now return to the question of their source. We face the same dilemma as in the Archimycetes and the Chytridiales. According to one concept, the Oomycetes are derived from the Algae; thus Bary (1884) considers the Chlorophyceae, especially *Vaucheria;* also Tavel (1892) names *Vaucheria* and related genera as ancestors but connects the Monoblepharidaceae with *Oedogonium;* Davis (1903) considers them derived from isogamous or slightly heterogamous Chlorophyceae at the stage of development which approximately corresponds with *Cladophora* and the isogamous Siphonales. According to the other concept, held by A. Fischer (1892), Dangeard (1906), Atkinson (1909*a*) and Scherffel (1925), the roots must be sought in the Chytridiales.

The fundamental question is whether the structure of the zoospores is of phylogenetic significance or not. Most authors have answered this question negatively; and yet one must admit that in the fungi where the number and insertion of the flagella have been accurately observed, they afford a systematic character with which other morphological facts entirely agree. Numerous ideas of this type have been recently upset by the fact that they have been based upon incorrect observations; thus Vuillemin (1907, contradicted in 1912) and Lotsy (1907) consider incorrect the observations of Hesse that *Pythium* is uniflagellate. Since then, it has been substantiated that he made his observations on abnormal material. Similarly Thaxter has described biflagellate Monoblepharidaceous zoospores which, according to Woronin (1904), belong to a parasite. Even the justification for *Myrioblepharis* (Thaxter, 1895) has been questioned by Minden (1915). Further the observation of Atkinson that *Pythium intermedium* may form two uniflagellate zoospores is inconclusive, because the fate of the halved zoospores is unknown and because Butler (1907) could not find this in the same (?) species; furthermore Dastur (1913) is inclined to consider abnormal similar phenomena which he observed in *Phytophthora parasitica.* It may easily be (and fungi offer several examples) that because of mode of life, parasitism etc., there appears a hereditary loss of flagella, but there is no suggestion that only one of two flagella is lost, and it is equally improbable that from two lateral flagella a terminal flagellum could arise, or *vice versa.* Hence it appears

justifiable to separate the uniflagellate forms (Monoblepharidaceae and Blastocladiaceae) from the biflagellate (Ancylistaceae, Saprolegniaceae Leptomitaceae and Peronosporaceae), the more so as other characters go parallel with the number of flagella. The uniflagellate zoospores are chiefly amoeboid, the biflagellate not; the uniflagellate families during growth give no cellulose reaction, the biflagellate always; the protoplasm in the former is often reticulate, in the latter homogeneous and periplastic.

The Oedogoniaceae or the Chytridiales are possible sources of the uniflagellate forms. The type of fertilization suggests the Oedogoniaceae but this family is much more highly organized and has multiflagellate zoospores and sperms. The uniflagellate condition of the zoospores and the habitual agreement of the Blastocladiaceae with *Macrochytrium* suggest the Chytridiales, only in this case, the sperm fertilization in *Monoblepharis* would be a new process. On account of the lack of intermediate forms, this difficulty seems greater than that which would arise in the derivation from Oedogoniaceous uniflagellate algae.

Derivation of the biflagellate forms is still more difficult. The Chytridiales, so far as known, can hardly be considered, as biflagellate forms have not been observed in them. Atkinson (1909) attaches *Lagenidium* to *Polyphagus*, and considers the Oomycetes and Zygomycetes have developed in parallel lines from the Ancylistaceae and those in turn from the Rhizideae; it is difficult, however, to support this connection between *Lagenidium* and *Polyphagus*. Similarly Scherffel (1925) considers an ascending series, from the Monadineae (Pseudosporeae) through the Archimycetes, Chytridiales and Ancylistaceae (*Ectrogella*) to the Saprolegniaceae, which has developed parallel with the algae under discussion. Direct derivation, however, from the Vaucheriaceae according to Bary and Tavel, or lower biflagellate Siphonocladiales and Siphonales according to Davis, is more satisfactory. The structure of the zoospores might be explained by the assumption of a new diplanetism and oogamous fertilization by the development of a conjugation tube. Besides, certain Leptomitaceae, *Rhiphidium* and *Araiospora*, show in habit and position of sexual organs, a striking similarity to the Vaucheriaceous *Dichotomosiphon*. As Atkinson has already emphasized, however, it is questionable whether much significance may be attached to this agreement; for there is a great possibility of convergence phenomena, *e.g.* in the Chlorophyceae, the Codiaceae have developed independently forms very similar to the Vaucheriaceae.

It seems to be the best solution to connect the Oomycetes with the Chlorophyceae. This is pure conjecture, however; the true ancestors in which separation took place have mostly died out and it is only by accident that analogies could be found on which to base conclusions. The finding of some new tropical species, however, might supply an entirely new point of view.

CHAPTER IX

ZYGOMYCETES

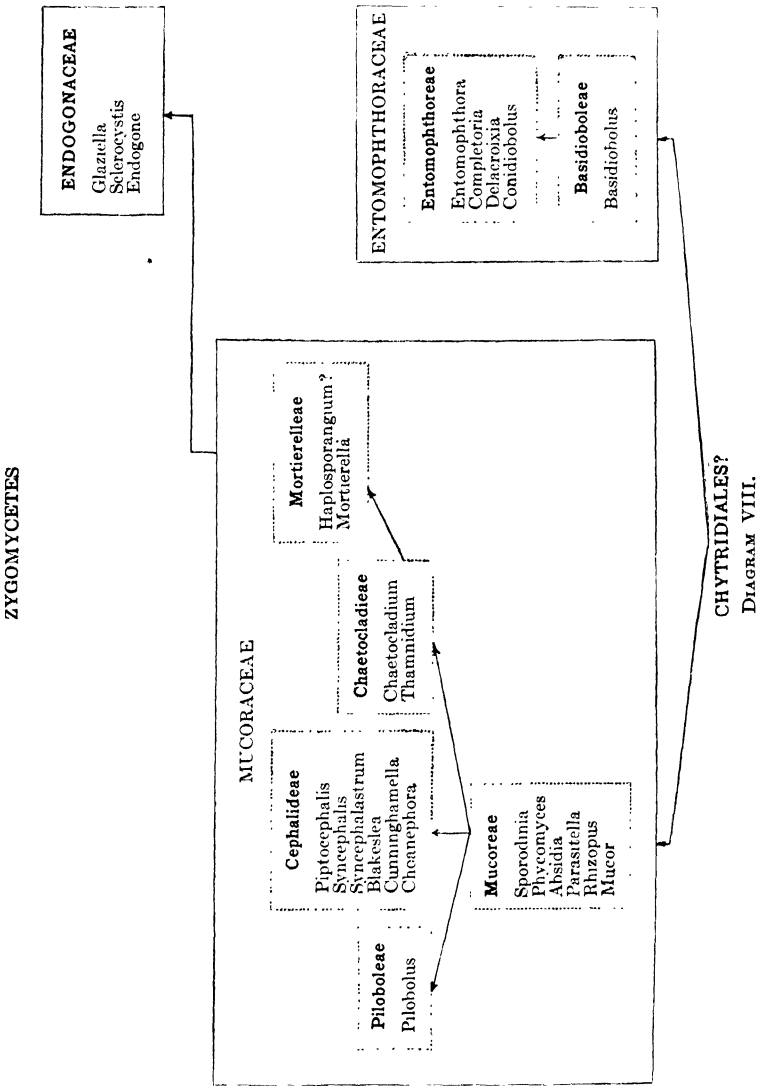
The Zygomycetes form an isogamous series, parallel to the Oomycetes, which has become adapted to terrestrial habitats. The thallus in the simple forms is coenocytic like that of the Oomycetes, in the higher forms, secondarily divided into cells. In several families, under certain conditions, the hyphae may fragment into oidia, hyphal bodies, etc., which develop further as sprout mycelia. Under unfavorable conditions, small portions of hyphae are thickened to gemmae.

The fructifications are aerial. The haploid portion produces sporangia, conidia and gametangia; the diploid, zygospores. The sporangia and conidia are each characteristic for a special developmental series. As in the higher Oomycetes, zoospore formation is absent. Instead the sporangia form non-motile, endogenous sporangiospores, while the conidia germinate by a single germ tube. While the conidia remain equivalent to each other, the sporangia, even within a single family, undergo fundamental changes and in various ways are reduced to conidia.

In both sporangia and gametangia, the individual daughter cells are no longer motile and the gametangia fuse, like those of the Oomycetes, in the coenocytic condition. The sexual act is essentially isogamous, in spite of heterothallism. The higher Zygomycetes tend more and more toward heterogamy. Within the gametangia in some Zygomycetes (as in the higher Oomycetes) there appears a tendency to privilege a few gamete nuclei; only in typical cases the division between functional and supernumerary nuclei occurs before the demarcation of the gametangia, so that the supernumerary nuclei may still migrate, while in the Oomycetes they are differentiated after the delimitation of the gametangia and then degenerate within them.

The products of the sexual act, the zygospores, are essentially different from the oospores of the Oomycetes in that their wall is itself formed by the gametangial wall while the walls of the oospores are new structures. In the higher Zygomycetes, especially in the Endogonaceae, between plasmogamy and fertilization (as in the Peronosporaceae), a short dicaryophase is inserted. In the Zygomycetes the development proceeds further and removes caryogamy both in time and place; for the first time in the fungi, caryogamy no longer occurs in the place designed for it (in the gametangia), but is retarded and shifted to an outgrowth of the female gametangium.

The relationships of the Zygomycetes are wholly obscure. Vuillemin (1886, 1912) and Lotsy (1907) connect the Zygomycetes through *Basidio-*



bolus to the Conjugales of the green algae and derive the Entomophthoraceae and Mucoraceae from the Basidioboleae. Davis (1903) considers in general terms the green algae, especially the isogamous

forms, which approximately correspond to *Cladophora* and the isogamous Siphonales. As intermediate forms are wholly lacking and apparently the morphological significance of simple structures like the Mucoraceous sporangium are still unknown, phylogenetic speculation is unfruitful. The present tendency is rather to connect the Zygomycetes with the Chytridiaceae or the more primitive Oomycetes. In the Chytridiaceae, the comparison of *Polyphagus* with *Conidiobolus* is suggestive, as is in the Oomycetes, a comparison with the Ancylistaceae, in which one needs only to imagine the absence of the conjugation tube in order to obtain a picture of a somewhat heterogamous zygogamy. It is quite probable that the Zygomycetes include phylogenetically heterogeneous organisms, which are only similar in the isogamous copulation of their coenocytic gametangia.

In their classification, the Zygomycetes fall into two series, one of which forms sporangia, the other conidia. The sporangial series includes the Mucoraceae and the Endogonaceae, whose difference lies in the degree of development of their fructifications. The conidial series includes the Entomophthoraceae.

Mucoraceae.—This family is mostly saprophytic on plant or animal remains, more rarely parasitic on other Mucoraceae or on higher plants and animals. Some forms, *e.g.*, *Mucor racemosus* and *M. mucedo*, may be regularly isolated from the air, others appear in the earth and form there in definite soils and definite associations. They are found in damp ground in coniferous forests, in Norway the principal species being *M. Rammannianus*, *M strictus*, *M. flavus* and *M. sylvaticus*. In cultivated ground occur *M. mucedo*, *M. sphaerosporus*, *M. racemosus*, etc. They play there a large part in the decay of organic substances (Hagem, 1907, 1910). A few species, because of special enzymes (*e.g.*, alcoholic fermentations by *M. javanicus*, or starch hydrolysis by *Rhizopus Oryzae*, have attained great technical importance (Wehmer, 1907). Still others, as *M. pusillus* and *Absidia Lichtheimi* (*M. corymbifer*), are important in medicine as they cause dangerous mycoses of internal organs.

The thallus corresponds entirely to that of the Oomycetes. It consists of ramose, coenocytic hyphae without septa; in old age and in the development of fructification, septa are formed irregularly to cut off the older vacuolate sections from the younger. An exception is *Haplosporangium*, whose hyphae early divide into numerous shorter or longer segments (Fig. 65). Furthermore, the hyphae of some genera in sugar solutions and anaerobic conditions break up into oidia (Fig. 54, 9) which develop further by sprouting; this sprout mycelium (Fig. 54, 4, 6 and 7), has ability to ferment in common with true yeasts. In *Mortierella* and *Syncephalis*, the hyphal branches fuse where they come in contact so that the mycelium frequently attains a reticulate appearance. Heterothallic species generally have no definite sexual dimorphism, the strains

usually differing slightly in physiological characters or the positive one is better developed.

Concerning the internal structure of the hypha, only a few details are known; thus the hyaloplasm of *Mortierella reticulata* and *Rhizopus nigricans* (Moreau, 1913) contracts into peculiar strands parallel to the hyphal axis. The nuclei are very small throughout (1 to 3μ in diameter). They divide simultaneously, both directly and indirectly, in the same hyphal region. The number of chromosomes is two.

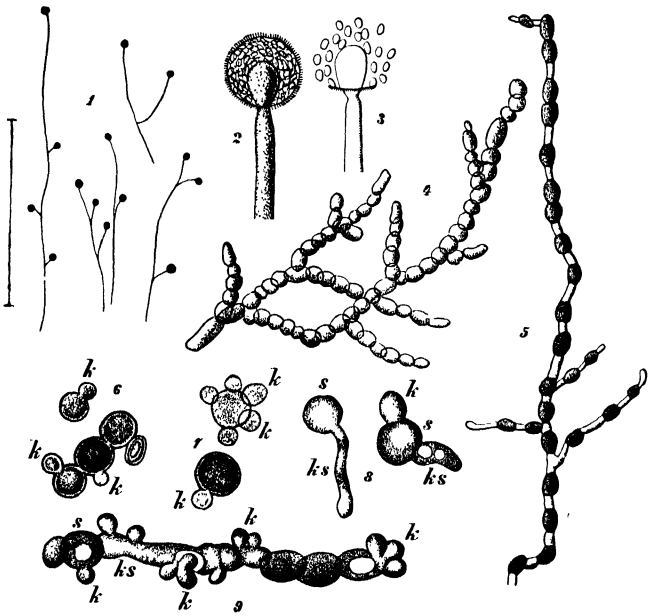


FIG. 54.—*Mucor racemosus*. 1. Sporangiophores. 2. Sporangium. 3. Opening sporangium with columella and collar. 4. Yeast-like cells. 5. Hyphae with gemmae. 6, 7. Sprouting cells; *k*, young sprout cells. 8. Sporangiospores with growing germ tube, *ks*. 9. Young hypha forming oidia and sprout cells. (1 × 2; 2, 3, 6 to 9 × 300; 4 × 120; 5 × 80; *after Brefeld, Pasteur and Reess.*)

The hyphae generally spread out evenly within and upon the substrate. *Rhizopus* and *Absidia* have more or less well-differentiated stolons consisting of a node, provided with appressoria or rhizoids (Fig. 55, 1); from the latter radiate new stolons. The rhizoids of the forms parasitic on other Mucoraceae are further modified; thus in *Mortierella Bainieri*, they grasp the host hyphae as claws or spirals, and in *Piptocephalis Freseniana*, penetrate the interior of the hypha and there branch into a small tuft of haustoria (Fig. 63).

Puzzling relations have developed in *Chaetocladium* and *Parasitella*. The mycelium of *Chaetocladium Brefeldi* var. *macrosporum* (Burgeff,

1920) stimulates the neighboring *Mucor* hyphae to greater branching and attracts them chemotropically. When a *Mucor* hypha reaches the neighborhood of a growing hypha of *Chaetocladium* they cling together. At the tip of the *Chaetocladium* hyphae, 3 to 8 nuclei collect and are abjointed after about half an hour (Fig. 56, *g*). After another half-hour the wall between the abjointed *Chaetocladium* cell and the *Mucor* hypha is dissolved and the *Chaetocladium* cell, which is also called a cupping cell, comes into direct communication with the *Mucor* hypha. Thereby, a portion of the *Mucor* protoplasm with nuclei enters the *Chaetocladium* cell (Fig. 56, *h* and *i*). The gall enlarges especially by the growth of

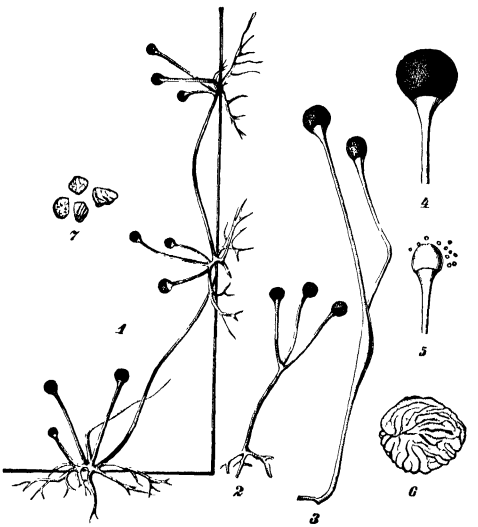


FIG. 55.—*Rhizopus nigricans*. 1. Stolons, rhizoids and sporangiophores. 2, 3. Single branched sporangiophores. 4. Sporangium. 5. Columella. 6. Sporangiospore showing the epispore. 7. Sporangiospore. (1, 2 × 8; 3 × 20; 4, 5 × 50; 6 × 1,200; 7 × 300; *after Vuillemin and Wehmer.*)

that part of the *Mucor* hypha; thus it absorbs much oil and protein-like substances from the *Mucor* and puts forth numerous short clavate or cylindric outgrowths whose tips again fuse with the *Mucor* hyphae and develop galls (Fig. 56, *k*). The *Mucor* nuclei, however, divide repeatedly and are found especially at the tip of the outgrowths and at the top of the galls. The hyphae of the *Chaetocladium*, which has been nourished parasitically, grow around the gall which is continually branching further, forming a cauliflower-like knob up to 0.5 mm. in diameter, from which, after approximately 24 hours, the first sporophores develop, completely emptying the gall.

While in *Chaetocladium* the reserve is accumulated in the gall itself and at a definite time is absorbed through the septum of the cupping cell,

Parasitella simplex (Burgeff, 1920) forms a special storage organ. Behind the cup, the hypha swells into a sac which is abjointed and surrounded by a thick wall (Fig. 56, *d*, 2) formed like the zygospore walls. As the processes in the formation of the cupping cells in these two genera are remi-

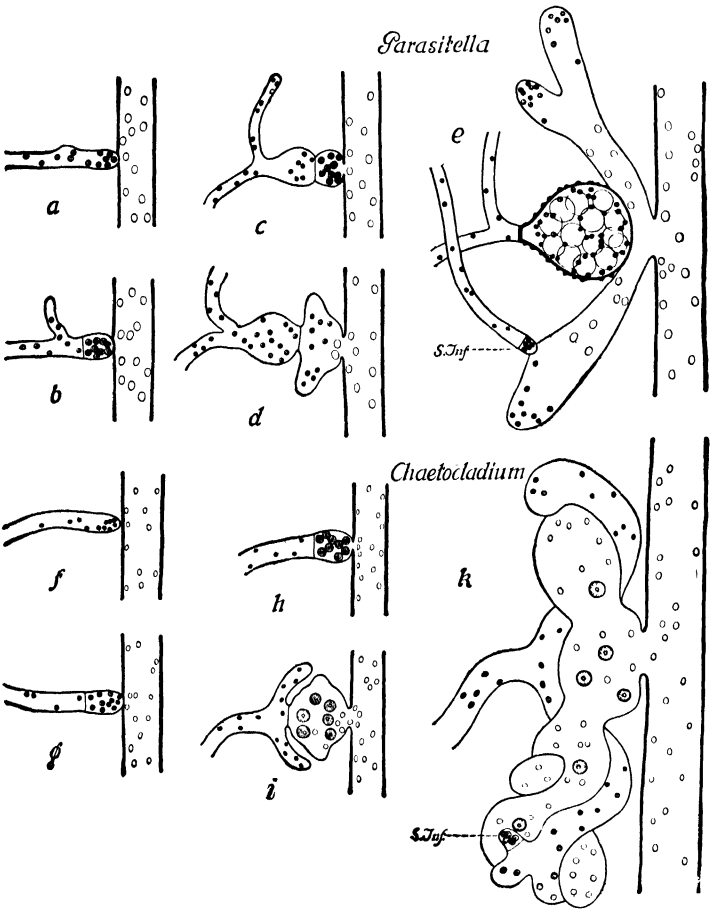


FIG. 56.—Diagram in one plane of the development of *Parasitella and Chaetocladium*. The nuclei of the parasite are shaded. *S. Inf.*, secondary infection. (*After Burgeff*, 1924.)

niscent of plasmogamy and as their parasitism is limited sexually, in that *Parasitella* + only parasitizes *Absidia glauca* − and *Parasitella* − only *Absidia glauca* +, Burgeff considers this type of parasitism to have arisen as a sexual function, perhaps an attempt at hybrid copulation.

As resting conditions, thick-walled gemmae are known (Fig. 54, 5), in *Mucor sphaerosporus* the mycelium may form true sclerotia. The

gemmae generally arise endogenously; multinucleate protoplasmic portions of varying circumferences, draw together and, inside the original hyphal membrane, surround themselves with a special thick wall. The stipitate gemmae (mycelial conidia, stylospores) of *Mortierella* and *Syncephalis* are cut off in scattered or racemose groups on short branches of the mycelium (H. Bachmann, 1900). Under suitable conditions both gemmae and sclerotia develop to new mycelia.

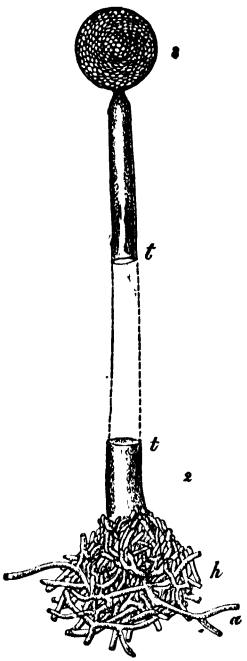


FIG. 57. — *Mortierella Rostafinskii*. Sporangiophore surrounded by hyphae, *h*, at base, *t*, in sheath; *a*, end of stolon. (× 100; *after Brefeld.*)

Asexual reproduction takes place through sporangia with sporangiospores. The parts of the mycelium from which the sporangia develop swell considerably and their nuclei divide repeatedly. In forms with stolons, the sporangiophores branch almost exclusively from the nodes (Fig. 55, l) and are then firmly attached to the substrate by the group of rhizoids; but in *Absidia* they branch directly from the stolons, midway between nodes. In *Mortierella Rostafinskii* (Brefeld, 1881) the rhizoids develop so luxuriantly that they surround the lower quarter of the sporangiophore like a thick sheath (Fig. 57); their outer wall is yellow or brown and cuticularized so that the whole structure looks like a capsule.

In the lower species, the sporangiophores are unbranched; in the higher species, they are forked, racemose, corymbose, cincinnal, etc. The tip of each branch swells up to a sporangium, allowing the protoplasm and nuclei of the swollen hyphal portion to migrate into it, and is finally abjointed. In the subfamily of the Mortierelleae, this septum is plane or slightly bent, like a watch glass; in the Mucoreae, Piloboleae, etc., it is arched far into the sporangium (Fig. 54, 2 and 3). This peculiar dome (columella) is generally smooth, cylindrical or pyriform and even after maturity of the sporangium remains clinging to the stipe. In *Pilobolus roridus* (Tieghem, 1875) and *Pilaira anomala* (Brefeld, 1881), a sporiferous hypha swells under the head into a large inflation on which the sporangium rests (Fig. 58, 1 and 2). On the absorption of more water, the sporophore bursts at the point of insertion of the columella and shoots out the sporangium and columella, often to a height of 1 m. and more, with an audible sound.

The wall of the sporangium in different tribes varies in chemical composition. In the Mucoreae the wall consists fundamentally of cellulose, which is subsequently so much incrusted with calcium oxalate crystals that it becomes fragile; simultaneously the cellulose is transformed

into an easily soluble form so that in damp air it dissolves and the crystals scatter. Only the base of the sporangial wall remains fixed in the majority of genera, forming a basal collar about the columella (Fig. 54, 3). In the Mortierelleae, the wall is equally soluble but the oxalate crystals are lacking. In the Piloboleae it is cuticularized, except at the base, and permanent.

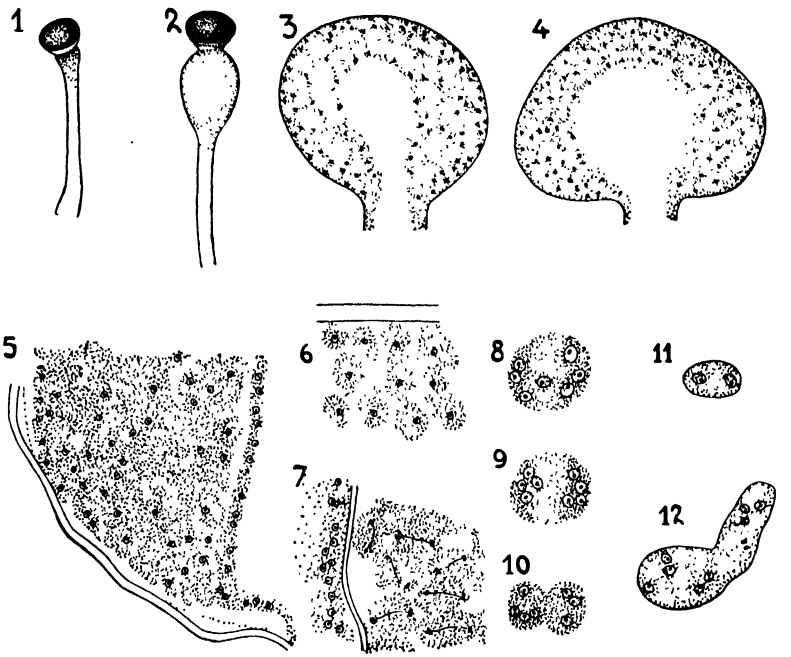


FIG. 58.—*Pilobolus crystallinus*. 1. Young sporangium. 2. Mature. 3. Showing protoplasm in young sporangium. 4. Beginning of vacuoles which later form the cleavage zone of the columella. 5. Differentiation of protospores. The wall of the columella will develop on the proximal side of the cleavage zone. 6. Protospores. 7. Nuclear divisions in the protospores, with wall of the columella at left beyond which is the superfluous protoplasm with nuclei. 8 to 10. Development of sporangiospores from proto spores. 11. Mature sporangiospores. 12. Germinating sporangiospores. (3 × 53; 4 × 20; 5 to 7 × 500; 8 to 12 × 830; *after Brefeld*, 1881, *and Harper*, 1899.)

At first most of the cytological processes within the sporangium are the same. The content of the young swelling is divided into a central zone mainly filled by sap and penetrated by a few protoplasmic threads, and into a rich peripheral zone containing most of the nuclei (Fig. 58, 3). The border between the two is differentiated into a foamy protoplasmic layer permeated by narrow flattened vacuoles. These fuse laterally and form between the vacuolate central portion and the protoplasmic spherical cap, a cleavage cavity (Fig. 58, 4); its bordering surfaces are covered

with a plasma membrane which is thickened into a wall on the side toward the stipe (Fig. 58, 7).

The central portion next the stipe remains sterile and becomes the columella. Its nuclei no longer show any membrane or nucleoli and degenerate, although occasionally fusions and amitotic divisions may appear. The peripheral spherical cap forms the fertile sporogenous layer.

Three types are distinguished according to the manner of spore formation. In the first type, *Pilobolus crystallinus*, (*P. microsporus*) and *P. oedipus* (Harper, 1899), the whole spore protoplasm is first split by vacuolization into uni-, rarely multinucleate, portions, the so-called protospores (Fig. 58, 5); these round off (Fig. 58, 6), swell, undergo several nuclear divisions (Fig. 58, 7) and are then divided into multinucleate portions by cleavage (Fig. 58, 8 to 10). These portions again round off, are surrounded with a membrane and become binucleate (Fig. 58, 11).

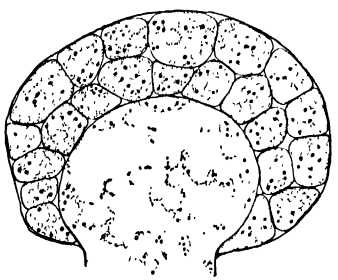


FIG. 59.—*Sporodinia grandis*. Vertical section through a mature sporangium. (*After Harper*, 1899.)

In *Circinnella conica* (Moreau, 1913) and *C. minor* (Schwarze, 1922) development is simpler; here the protospores without further splitting are surrounded by membranes and become spores directly. In most of the other genera, as in *Sporodinia* (Harper, 1899) *Phycomyces*, *Rhizopus*, *Mucor*, *Absidia* and *Zygorhynchus* (Swingle, 1903; Moreau, 1913; Green, 1927) the protospore stage is omitted. The division of the nuclei in *Phycomyces*, probably also in the other genera, occurs simultaneously in the whole sporangium. Then the sporogenous protoplasm splits directly into multi-, rarely uninucleate portions which round off, surround themselves by a membrane and develop directly to spores without further nuclear division (Fig. 59).

The sporangiospores are unicellular, generally ellipsoidal or spherical, hyaline or dully colored; they lie either free in the sporangium or are embedded in a finely granular intermediate substance, swelling gel-like in water, which is probably developed within themselves (Fig. 5, 2). At germination they swell considerably and develop into a mycelium through one or more germ tubes. Their morphological characters are not yet clear. One can either regard them as analogous to the zoospores of the Oomycetes, *i.e.*, as akinetes which because of incomplete cleavage have remained large and multinucleate; or one can, probably with more reason on the basis of the parallelism in protospore formation between *Pilobolus–Sporodinia* and the *Synchytrium decipiens–S. Taraxaci* series, regard the sporangiospores as reduced sporangia and the *Mucor* sporangia are reduced sori. As in *Synchytrium* and *Urophlyctis alfalfae* the contents

of the sori, are differentiated into individual sporangia which, because of the transition to terrestrial habitats, germinate with germ tubes instead of zoospores. According to this explanation the import of columella formation remains obscure.

The original sporangial type discussed above, represented by *Mucor*, *Sporodinia*, etc., in the higher forms is modified in two directions, either the individualization of oospores is retarded without being entirely suppressed as in the Oomycetes, or the sporangia decrease successively in differentiation, size and spore number and finally sink to conidia in appearance and function.

In the direction of retardation of spore formation, undoubtedly the *Choanephora–Piptocephalis* series must be indicated. In poorly nourished *Choanephora cucurbitarum* sporangiophores and sporangia similar to those of *Mucor* are formed. The ends of the brown, smooth sporangiospores

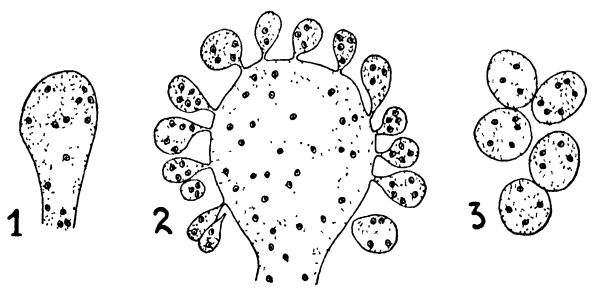


FIG. 60.—*Cunninghamella echinulata* Development of sporangiophores. (× 740; *after Moreau*, 1914.)

have two to three hyaline processes from each of which up to 20 hairs arise. With liberal food, on swollen tips of vertical hyphae or eventually on the short secondary branches, the spores arise, not endogenously by cleavage, but exogenously by budding. Spore formation is ontogenetically retarded and is transferred from the interior of the sporangium to its upper surfaces. These exogenous spores, in contrast to the endogenous, are longitudinally striate (Wolf, 1917).

This exogenous spore formation may be seen in *Cunninghamella* cytologically investigated by Moreau (1913). In *C. echinulata* and *C. Bertholletiae*, the ends of the sporophores swell, like sporangia, into sacs (Fig. 60, 1), whose content is differentiated into a watery inner and a rich outer zone. The peripheral layer splits, not into spore initials, as *Sporodinia*, but allows the protoplasm to pass out into small spherical sacs, sessile on short sterigmata, with three to eight nuclei each. These sacs are cut off and transformed to spores (Fig. 60, 2) corresponding in size and form to the typical Mucoraceous spores but borne on the outer surface of the sporangia instead of within them.

This developmental series finds its continuation in *Blakeslea trispora* (Thaxter, 1914*a*). This species, also as *Choanephora*, forms under certain conditions of growth, *e.g.*, in saturated atmosphere, typical multispored *Mucor* sporangia with large pyriform columellas (Fig. 61, 1). These sporangia show a marked tendency toward degeneration: with slight alteration of cultural conditions, they decrease in cross section and spore number, the columella becomes smaller and disappears (Fig. 61, 2) and there result forms, which only distantly resemble the original sporangium.

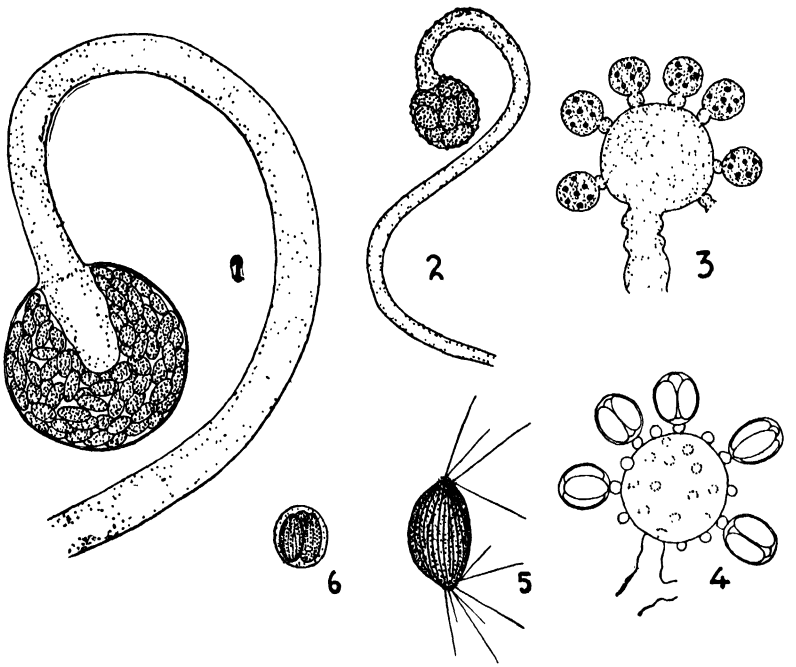
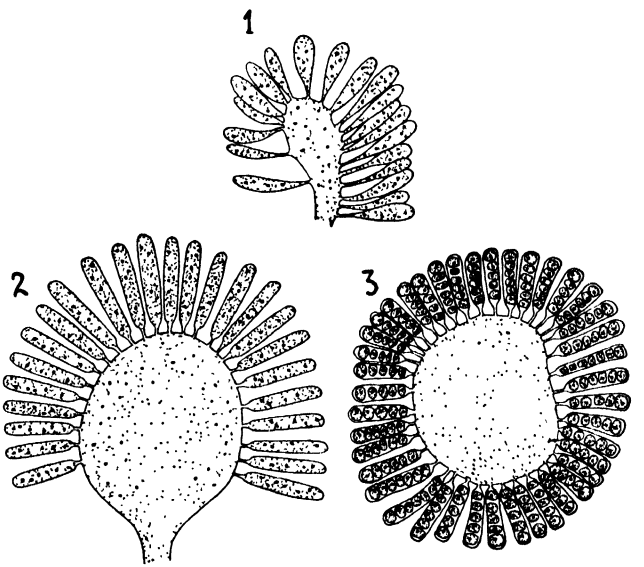


FIG. 61.—*Blakeslea trispora*. Modifications of sporangia. 1. Original form. 2. Reduced form without columella. 3, 4. Formation of exogenous sporangioles. 5. Sporangiospore from sporangiole. 6. Mature sporangiole with broken sterigma. (1 to 4, 6 × 260; 5 × 720; *after Thaxter*, 1914.)

Under normal conditions of growth, the spore protoplasm migrates from the sporangium into saccate protrusions, sessile on spherical sterigmata (Fig. 61, 3) and there, by meridianal splitting, divide into three spores each (Fig. 61, 4) which, as in *Choanephora*, bear little tufts of hairs at their tips (Fig. 61, 5). At maturity, the protuberance is separated from its sterigma or with its sterigma from the sporangium and is disseminated (Fig. 61, 6). In this species, spore formation (in contrast to *Cunninghamella*) is again retarded; between the differentiation of sporangial content into a sterile and a fertile zone and the individualization of the

ingle spores, the sporangium also continues its development and evelops into numerous extrasporangial partial sporangia, each of which orms a small number of sporangiospores.

In *Syncephalastrum racemosum* and *S. cinereum* (Thaxter, 1897; Moreau, 1913) the facultative formation of *Mucor* sporangia is entirely ost; the extramatrical partial sporangia have reached a higher stage of evelopment. They develop several sterigmata, generally joined palmtely into long cylindrical tubes which take up as many as 20 nuclei Fig. 62, 1 and 2). When they have attained their full length, their ontent splits simultaneously into uni- or multinucleate portions which



IG. 62.—*Syncephalastrum cinereum*. Development of extrasporangial partial sporangia. (× 740; *after Moreau*, 1914.)

ound off and are surrounded by membranes (Fig. 62, 3). These are berated by disintegration of the sporangial membrane.

In *Syncephalis*, development goes still further (Tieghem, 1875; Guillemin, 1902). After the destruction of the partial sporangium, the pores always remain connected with the adjacent cuff-like part of the porangial membrane; the spore wall itself remains thin and insignificant hile the sporangial wall is thick and occasionally sculptured. In *S. urantiaca*, the partial sporangia divide by septa into as many locules s there are spores. By splitting these septa, they divide into oidial iembers, each of which contains a spore; thus the spores are completely urrounded by a sporangial wall, inseparable from their own wall.

In all these genera, the sporangium which has become functionless, remains in open connection with the sporiferous hyphae; it retains its more or less definitely capitate shape and collapses only after maturity of the partial sporangia. It has degenerated only in so far as the sterile inner part is no longer separated from the peripheral spore protoplasm by a columellar wall. In *Piptocephalis* it also takes part in the development; it loses its typical capitate form, and shrinks to a verrucose basal cell (Fig. 63) bearing at its top the partial sporangium which is freed

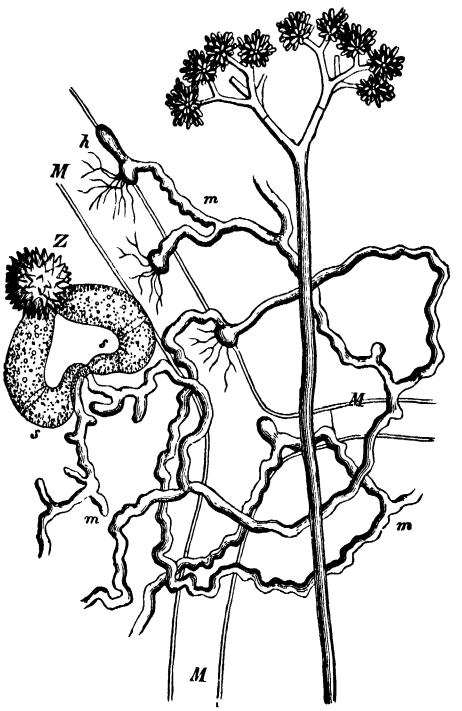


FIG. 63.— *Piptocephalis Freseniana*. *m*, mycelium with haustoria, *h*, which penetrate the hyphae, *M*, of *Mucor Mucedo*; *Z*, zygospore with its two suspensors, *S*. Conidiophore at the right. (*After Brefeld.*)

from the sporiferous hypha by its degeneration (Brefeld, 1872; Tieghem, 1875). The partial sporangia, as in *Syncephalis aurantiaca*, break up into monosporous members in which the sporangial membrane is fused with the spore membrane and is externally almost indistinguishable from it. The sporangiophores, therefore, have been changed into conidiophores which may be recognized as original sporangiophores only by their phylogeny.

The catenulate spores of *Piptocephalis*, which correspond to the sporangiospores of *Syncephalastrum* plus the section of the surrounding

sporangial wall, and the monosporous members of the partial sporangia of *Syncephalis*, do not fall under the scholastically narrow concept of conidia and have been described by new terms. As none of these is very fortunate, and as the differences really possess no important principle, it seems preferable to employ here also the term conidia, which already includes structures very different phylogenetically; it is essential to keep in mind that these parts have resulted by the fragmentation of extrasporangial partial sporangia.

All these phenomena, especially in genera like *Choanephora* and *Blakeslea*, besides their actual interest, have a fundamental significance for the comprehension of the higher fungi; for they show that the change of nutritive conditions produce different types of fructifications which externally are so different from each other that the determination of their relationships can only be obtained in pure culture.

The *Thamnidium–Chaetocladium* and the *Mortierella–Haplosporangium* series departs farther from the fructification of the Mucoreae than the *Choanephora–Piptocephalis* series. In the latter, the number of sporangiospores remains unaltered; only they no longer are endogenous in the sporangia, but are somewhat retarded and in a certain sense exogenous in the germination of the partial sporangia, so that in the highest forms they remain enclosed in these partial sporangia. In the *Thamnidium–Chaetocladium* series, however, the sporangiospores are numerically much reduced; their functions are assumed by the sporangia and these themselves successively degenerate to conidia.

In *Thamnidium elegans* the main axis possesses an apical multispored sporangium which, like that of *Mucor*, has a columella (Fig. 64, 1 and 2, *a*). Under definite conditions dichotomous branches terminating in sporangia are formed from the main axis. These sporangia, however, are smaller than the terminal, have no columella, become loosened as a whole from the sporangiophores and contain only a few, generally four spores (Fig. 64, 2 and 4). These are liberated not by deliquescence but by disintegration of the sporangial membrane. These reduced sporangia are called **sporangioles.** The spores in both types of sporangia behave similarly in their germination and further development. Under favorable conditions of nourishment, however, they are continued through several generations when the sporangioles become as large and multispored as the sporangia. Conversely, with poor nourishment the terminal sporangia change into sporangioles whose spore number is often reduced to one (Tavel, 1892). Since within the same species both well-developed and reduced sporangia appear, *Thamnidium elegans* corresponds to the genera *Choanephora* and *Blakeslea* in the *Choanephora–Piptocephalis* series; only in the latter both sporangial types arise separately on special sporangiophores while in *T. elegans* they are formed on the same sporangiferous hypha.

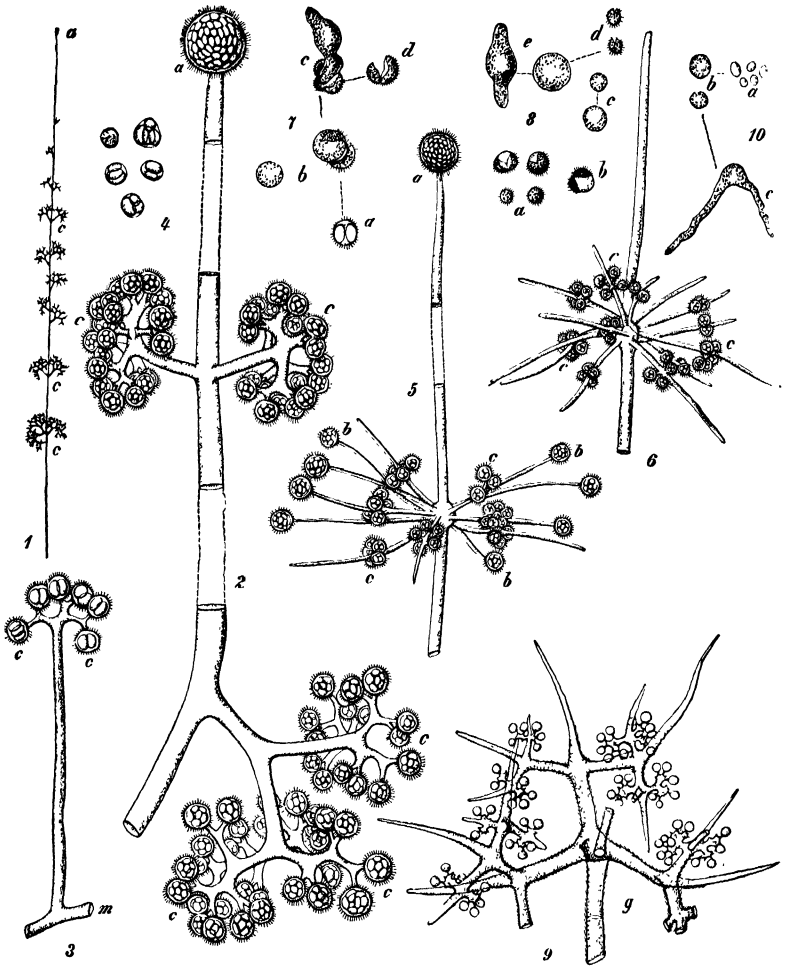


FIG. 64.—*Thamnidium elegans*. 1. Habit. *a*, terminal sporangium; *c*, the sporangioles. 2. Same, more enlarged. 3. Smaller sporangiophore bearing few-spored sporangioles, *c*; *m*, portion of hypha. 4. Sporangioles. *Chaetostylum Fresenii*. 5. Sporangiophore with terminal sporangium, *a*, and sporangioles, *c*; borne on branches which either terminate in a sporangium, *b*, or are sterile. 6. Sporangiophore producing only sporangioles, *c*; tips of main axis and branches are sterile. 7. Germination of sporangiole, *a*; leaving the sporangium, *b*; formation of germ tube, *c*; empty spore wall, *d*. *Chaetocladium Jonesii*. 8. Germination of sporangia with single spores *a* to *d*. *Chaetocladium Brefeldii*. 9. Conidiophore with conidia, the tips of the branches sterile. 10. Germination of conidia. (1 × 6; 2, 5, 6 × 120; 3, 4 × 200; 7, 8 × 300; 9, 10 × 450; *after Brefeld.*)

This line of development is continued through *Chaetostylum Fresenii Thamnidum chaetocladioides*). Here, under unfavorable conditions of nourishment, the terminal sporangia abort (Fig. 64, 6) and only with adequate nourishment again bear true apical sporangia (Fig. 64, 5).

In these two species the terminal sporangia already have declined n number, as the sporangioles predominate, while in *Chaetocladium* hey disappear entirely, never to reappear. In this genus, the sporangioles also degenerate. They become monosporous so that the spore walls coalesce with the sporangial wall. In *Chaetocladium Jonesii*, this double nature of the spore wall is evident in germination; here the sporangial wall is thrown off as exospore and the spore lies free at germination Fig. 64, 8). In *C. Brefeldii*, however, this differentiation is suppressed nd the monosporous sporangium puts forth its germ tubes directly Fig. 64, 10). Thus the sporangium is here entirely transformed into a conidium (Brefeld, 1872; Tieghem and Lemonnier, 1873).

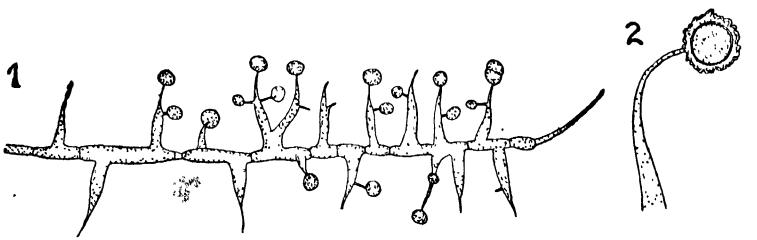


FIG. 65.— *Haplosporangium bisporale*. 1. Sporangiferous hypha. 2. Monosporangium with a single sporangiospore. (× 720; *after Thaxter.*)

Mortierella and *Haplosporangium* show a similar degeneration. In *Mortierella* the sporangium, like the sporangioles of *Thamnidium*, is separated by a basal septum from its sporangiophores; there is no differentiation of its content into sterile and fertile zones and the spores arise directly by cleavage of the whole protoplasm. Their number decreases notably and in some species is only two to four (Tieghem and Lemonnier, 1873). In *Haplosporangium bisporale* (Thaxter, 1914*a*) this condition has become the rule. Here the sporangia remain very small nd retain only one or two spores (Fig. 65, 1). The spore wall is delicate, the sporangial wall thick and sculptured; unrelated to *Thamnidium* nd *Chaetocladium*, here the same process has taken place and has led o one- or two-spored sporangioles, biologically regarded as conidia.

In a biological sense, *Thamnidium–Chaetocladium* and *Mortierella–Haplosporangium* form a series parallel to *Pythium–Peronospora* under he Oomycetes. Only in the Oomycetes, reduction of the sporangia to a single spore has resulted from inhibition of zoospore formation, *i.e.*, it has remained a purely internal process which has had no direct reaction on the form and size of the sporangia themselves; thus the conidia of

Peronospora are just as important as the sporangia of *Plasmopara*. In the Mucoraceous series, the primary import does not lie in an inhibition of formation of spores whose individuality is retained but in a degeneration of sporangia. A decrease in size of the sporangia leads to a decrease in the number of spores. Biologically, the result is the same in both cases: a single conidium replaces sporangia with many spores.

Besides this asexual reproduction, in most Mucoraceae sexual organs are known. In the homothallic forms their appearance is mainly depend-

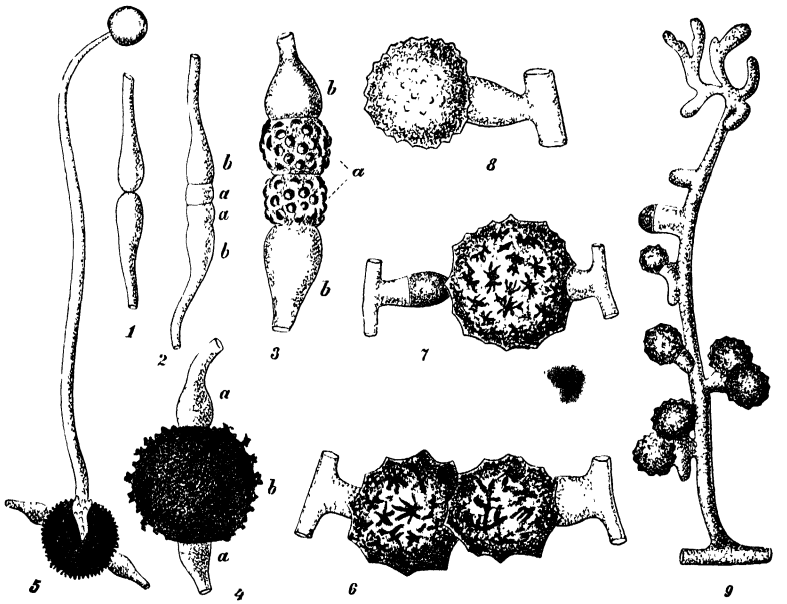


FIG. 66.—*Mucor Mucedo*. Zygospore formation. 1. Two copulation branches approach. 2. Separation of gametangia, *a*, from suspensors, *b*. 3. Formation of azygospores instead of copulation. 4 Mature zygospore, *b*, between the suspensors, *a*. 5. Germination of zygospore. (1 to 4 × 225; 5 × 60 *after Brefeld.*) *Mucor erectus*. 6, 7. Azygospore formation. *Mucor tenuis*. 8, 9. Azygospores. (*After Bainier.*)

ent on conditions of nourishment; the heterothallic forms require the presence of both sexes. Mycelia of one sex may be cultivated alone for any number of "generations" without the appearance of normal sexual organs, which appear promptly whenever the opposite sex is brought into the vicinity.

If two sexually mature (in heterothallic forms also dynamically opposite) hyphae come in contact with one another under favorable conditions, each forms an outgrowth toward the other (Fig. 66, 1). This is cut off from the sporiferous hyphae close behind the tip by a diaphragm-like wall laid down from the edge inwards (Fig. 66, 2). The tip cell is

the gametangium, the sporiferous hypha is the **suspensor** and the whole outgrowth is called copulation branch. As the homothallic forms are bisexual, there apparently takes place in their hyphae, at the formation of the copulation branches, a spatial separation of + and − energids. In some forms, the copulation branches may arise from ordinary hyphae; in others they are formed on special branches, the **zygophores.**

The separating double wall between the gametangia is gradually dissolved from the middle toward the edge and the zygote becomes a hypnospore by the formation of a many-layered wall, the **zygospore** (Fig. 66, 4). If in the homothallic forms, the copulation branch finds no mate, in many species the gametangium is surrounded by a many-layered wall, and is called an **azygospore** (Fig. 66, 8 and 9) or chlamydospore. The same thing occurs if the cultures are removed to unfavorable conditions, such as high temperatures. In the heterothallic forms similar phenomena may occur if the copulation branches belong to two different species; in this case they cease growing and transform the gametangia (in case they have already been cut off as such) into azygospores. This incomplete hybridization, however, does not seem to occur between all species, for it occurs between *Phycomyces nitens* + and *Mucor Mucedo* − and conversely, but not between *Phycomyces nitens* and *Rhizopus nigricans* (Blakeslee, 1904, 1915, 1921, 1927).

While both gametangia are usually of the same size and thus externally suggest isogamy, in individual species their size relationships show a notable tendency to heterogamy. Thus in the homothallic *Zygorhynchus Moelleri*, the copulation branches are unequally developed. In the heterothallic *Absidia Orchidis*, the gametangia are unequally broad, so that the zygospore is conical. In *Piptocephalis*, the zygospores grow upward from the point of fusion so that it is borne upon the top of the copulation branch (Fig. 63). In *Syncephalis nodosa*, one copulation branch coils around the other in a helix (Thaxter, 1897); the zygospore does not arise at the point of fusion but comparatively distant, on the outer wall of the helix near the septum separating the gametangium from the suspensor. Still more puzzling is *Dispira americana* (Thaxter, 1895*a*), parasitic on other Mucoraceae, where, at the tips of the vegetative hyphae, thicker fertile branches swell and approach the sporangiophores of the host, forming small sinkers. A septum divides the swollen part into two cells, both gametangia. After copulation the proximal cell swells and changes to a zygospore which is surrounded with digitate processes of the distal cell.

All these phenomena may be referred to a unified basic form as soon as one considers the cytological relationships. As an example may serve the homothallic *Sporodinia grandis* (Leger, 1895; Dangeard, 1906; Lendner, 1908; Moreau, 1913; Keene, 1914). Its young gametangia contain more than a thousand nuclei (Fig. 67, 1). While the separating wall

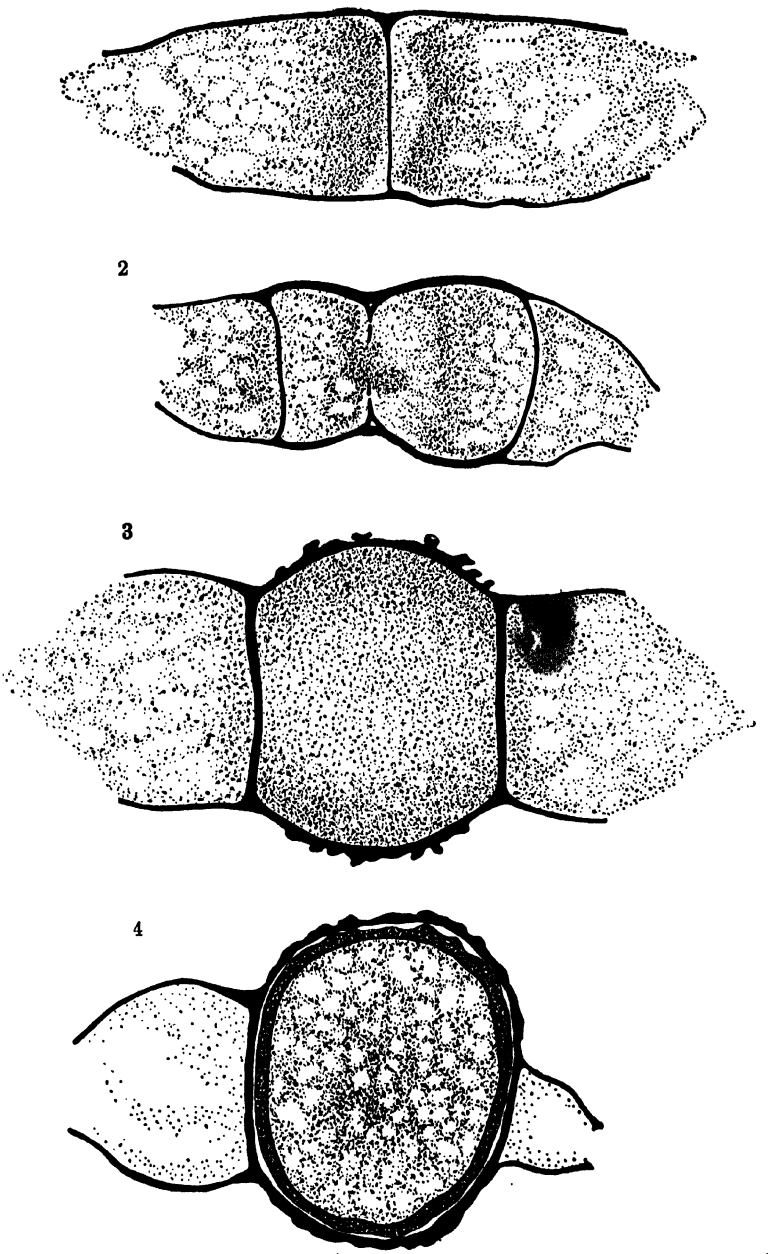


FIG. 67.—*Sporodinia grandis*. Development of zygospores. (× 124; *after Keene*, 1914.)

between the gametangia is dissolved, the nuclei undergo a division almost simultaneously; their cytoplasm intermingles (Fig. 67, 2) and their nuclei subsequently pair and fuse. Those without mates, especially those near the periphery, degenerate and disappear. Meanwhile at the surface, a wall of several layers has been formed, the suspensors collapse and the zygospores presently lie free upon their substrate (Fig. 67, 3 and 4.)

It is characteristic of this process that no dynamic differentiation occurs between the + and − energids in spite of their separation in space. Thus both gametangia are cytologically equivalent, and fertilization is isogamous with reference to the nuclei. In *Sporodinia*, as in the higher Oomycetes, there is no individualization of gametes, so that two coenocytic gametangia copulate and accomplish, as in *Albugo Bliti*, a multiple nuclear fusion, *i.e.*, several fertilizations. Thus the zygospore of *Sporodinia* is not a simple zygote like that of *Olpidium* but is the product of two coenogametes, a coenozygote or zygosporangium.

All other Mucoraceae so far investigated conicide with *Sporodinia grandis* in their essential cytological relationships, *e.g.*, *Mucor* (Dangeard, 1906; Moreau, 1914), *Rhizopus*, *Absidia*, *Phycomyces* and *Zygorhynchus* (Moreau, 1914, contradicted by Gruber, 1912). In *Zygorhynchus Dangeardi*, all gametic nuclei but four degenerate in the young zygote. The surviving nuclei [redacted] pairs very late, after the endospore has been formed. A similar retardation of caryogamy has been observed in *Phycomyces nitens* (Burgeff, 1915), in which the nuclei in the zygospores, 5 months old and ready to germinate, still lie arranged in pairs. Perhaps tendencies similar to those which cause a retardation of nuclear fusion in the oospores in the Peronosporeae are present in the Mucoraceae. In spite of external heterogamy, *Absidia* and *Zygorhynchus* copulate just as *Sporodinia*, and hence are dynamically isogamous and partially homothallic.

The wall of the zygospores in the more carefully studied species of *Mucor*, *Sporodinia* and *Zygorhynchus* consists of five layers (Vuillemin, 1904). The innermost is thin and granular; it forms the transition from the protoplasm and, to a certain extent, is the mother layer. The next is thickest and called the cartilaginous layer on account of its elasticity. This is covered by a thin sheath, the middle cuticular layer. The fourth, or carbonaceous layer, is fragile and brown or black; the outermost cuticular layer is either pale and elastic, or dark and fragile, and often interrupted or fractured. The greatest modifications in the various genera are shown by the relief of the carboniferous layer, which is verrucose or reticulate. The two outer layers are grouped as exospore, the three inner as endospore.

In *Absidia* and *Phycomyces*, the zygospores are loosely surrounded by echinulate branches of the suspensors. In *Mortierella*, these branches

intertwine with the neighboring hyphae into a solid felt whose outer surface is cuticularized and brown. Within this tissue lies the zygospore. Thus in *Mortierella*, for the first time in Phycomycetes, a true fructification is formed, in Brefeld's terminology, a carpospore.

The zygospores germinate only after a long resting period. The exospore is ruptured, the endospore puts forth a germ tube which develops to a mycelium or, with insufficient nourishment, directly to a sporangium (Fig. 66, 5) or a conidiophore.

During germination, meiosis of the diploid nuclei occurs. Where the germ tube becomes the fundament of a sporangium (*e.g.*, *Phycomyces nitens;* Burgeff, 1915) meiosis only occurs in the latter which is called a germ sporangium and, as we shall see later, is the precursor of the ascus. The sexual relationships existing at meiosis have been more closely studied for three types (*Sporodinia, Mucor Mucedo* and *Phycomyces nitens;* Blakeslee, 1904, 1906). In *Sporodinia* the sporangiospores are homothallic and the separation of the + and − energids occurs only in the formation of the copulation branches. This life cycle may be represented in the following scheme which corresponds in its fundamental characters to that of *Polyphagus* and *Saprolegnia:*

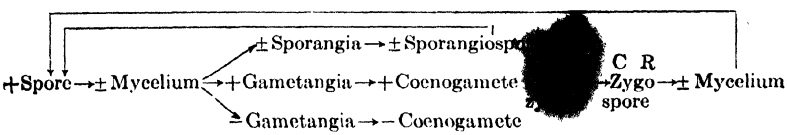


DIAGRAM IX.

In the heterothallic *Mucor Mucedo*, the separation of the + and − energids occurs probably in the formation of sporangia; *i.e.*, the spores are all of one sex in one sporangium and are all + or all −:

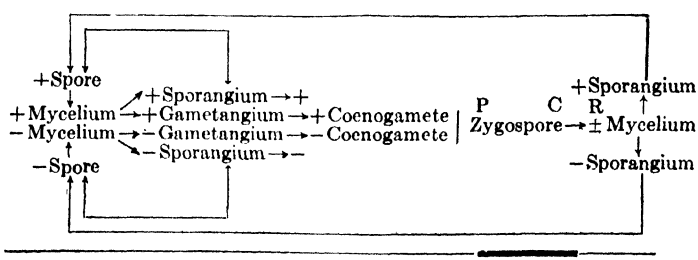


DIAGRAM X.

In the equally heterothallic *Phycomyces nitens*, the separation of sexes occurs only in the formation of spores. Even so, it is incomplete: besides the + and − spores, there are also unstable, neutral, bisexual spores in

whose sporangia the separation into + and − spores is continued (Burgeff, 1912):

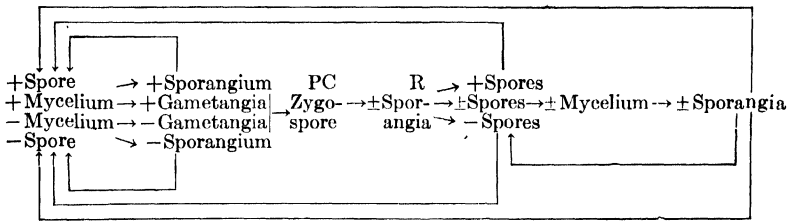


DIAGRAM XI.

The systematic classification of the Mucoraceae is based on the asexual organs of fructification; but since these merge into one another through numerous transitional forms, the dividing lines are drawn by various authors in entirely different places. Four tribes should be mentioned: the Mucoreae, Cephalideae, the Chaetocladieae and the Mortierelleae.

The Mucoreae (including Piloboleae) are characterized by a completely developed sporangium provided with a typical columella. They include *Mucor*, *Rhizopus*, *Sporodinia*, *Absidia*, *Phycomyces*, *Zygorhynchus* and *Parasitella*. They are generally saprophytic on all possible substrates, but *Sporodinia* occurs mostly on pileate fungi; *Parasitella* alone is preponderantly parasitic on other Mucoraceae.

The Cephalideae are distinguished from the Mucoreae by the retardation of spore formation which generally occurs in the extrasporangial partial sporangia. They include *Choanephora*, *Cunninghamella*, *Blakeslea*, *Syncephalastrum*, *Syncephalis* and *Piptocephalis*. *Choanephora* is a feeble parasite on wilted floral organs of many phanerogams, *e.g.*, *Cucumis*, *Hibiscus* and *Gossypium*, and causes in part a rotting of the fruit; *Piptocephalis* is parasitic on other Mucoraceae, the other genera are saprophytic.

The Chaetocladieae form a series parallel to the Cephalideae. They are characterized by the increasing degeneration of the sporangium. Of the genera here discussed, they include the saprophytic *Thamnidium* and *Chaetocladium*, which is generally parasitic on other Mucoraceae.

The Mortierelleae, finally, are marked by the absence of a columella and by their ability to form fructifications. The only well-known genus, *Mortierella*, is generally saprophytic; *M. Bainieri* is parasitic on Basidiomycetes. The genus *Haplosporangium*, which perhaps also belongs here, is saprophytic.

Endogonaceae.—On account of the structure of their sporangia and the formation of fructifications, this family is closely connected to the Mortierelleae; in contrast to the latter, however, the relationships of

the sporangia and zygospores have not been experimentally determined. *Endogone* is saprophytic and generally subterranean, while *Sphaerocreas*, *Sclerocystis* and *Glaziella* are lignicolous. The thallus consists of multinucleate hyphae often anastomosing and becoming septate in age.

The sporangia, formed in special fructifications (sporangiocarps), are known only in *Endogone reniformis* and *E. malleola.* These consist of a thick, solid, whitish-yellow pseudoparenchyma (Fig. 68, 1) which may attain a considerable size, up to 2 cm., and at times possesses a definite form (*e.g.*, reniform in *E. reniformis*). In the rind layer or in special sporiferous hyphae radiating in all directions, terminal or intercalary Mucoraceous sporangia are formed. As in *Mortierella*, their contents split into regular portions and finally flatten polyhedrally from

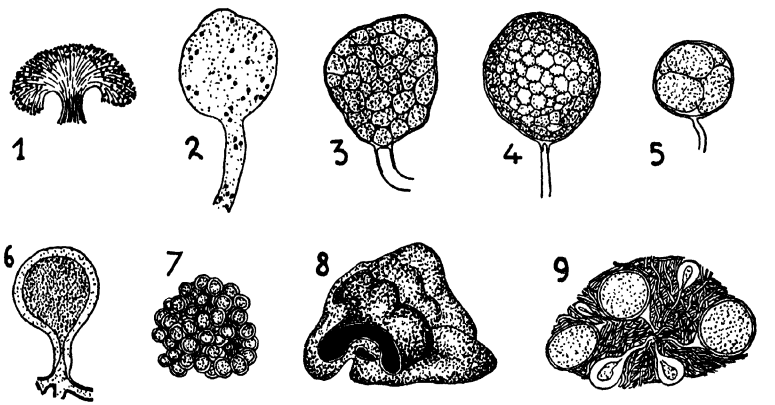


FIG. 68.—*Endogone malleola.* 1. Longitudinal section of a sporangial fructification. 2. Young sporangium. 3. Section of mature sporangium. 4. Mature sporangium. *Endogone reniformis.* 5. Mature sporangium. *Endogone fasciculata.* 6. Young chlamydospore. 7. Fascicle of chalmydospores. *Glaziella aurantiaca.* 8. Hollow chlamydosporic fructification. 9. Group of chlamydospores in ground tissue. (1 × 12; 2 to 6 × 370; 7 × 67; 8 reduced; 9 × 36; *after Bucholtz*, 1912, *and Thaxter*, 1922.

lateral pressure (Fig. 68, 2 to 5). The spores germinate with one or several germ tubes (Bucholtz, 1912; Thaxter, 1922; Walker, 1923).

The zygospores are also united into fructifications and arise mostly inside the whitish or yellowish tuberiform hyphal knots up to the size of a hazelnut (Fig. 69, 9), which in some species contain latex organs. At present the youngest known stage of these fructifications consists of a comparatively thick tissue of ramose hyphae which at the periphery are closely intertwined and form a sort of peridium. In the ground tissue, there appear a large number of pairs of copulation branches whose development proceeds approximately simultaneous throughout the fructification.

In the only species whose sexual reproduction is well known at present, *E. lactiflua* (Bucholtz, 1911, 1912), the copulation branches arise mostly

at the ends of hyphae or of their branches (Fig. 69, 1–2). On their surfaces they form very thin, rapidly tapering processes which later, because of the enlargement of the copulation branch, are shoved aside or toward the base. These are probably the fundaments of the hyphae which surround the zygospores at maturity.

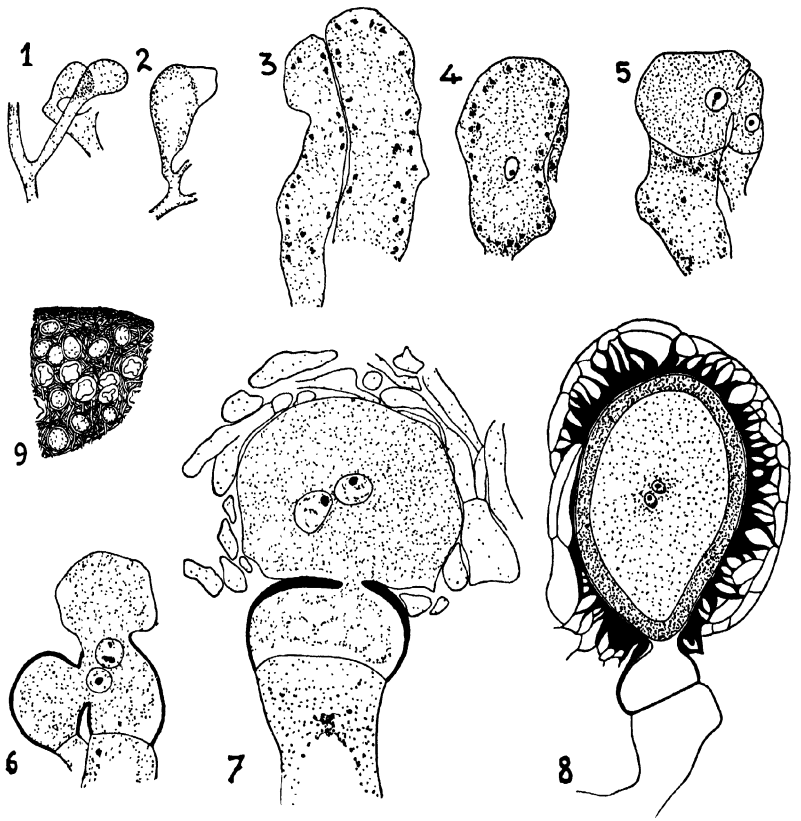


FIG. 69.—*Endogone lactiflua*. 1. Young copulation branches in contact. 2. Single copulation branch. 3. Two gametangia with numerous peripheral nuclei. 4. Large central nucleus in the female copulation branch. 5. Formation of copulation opening. 6. Nuclear migration. 7. Formation of hyphal sheath around zygote. 8. Zygote still connected with gametangia. *Endogone incrassata*. 9. Section of sporocarp with peridium and gleba. 1, 2 × 400; 3 to 5, 7 × 630; 8 × 370; 9 × 10; *after Bucholtz*, 1912, *and Thaxter*, 1922.)

The female copulation branch is somewhat larger and bent at the base. The copulation branches press together and bend around so that the male is surrounded by the female. Their content is granular and multinucleate. The nuclei are arranged peripherally (Fig. 69, 3) and undergo a simultaneous division, after which, in the center of the game-

tangium, there is a large nucleus which probably has migrated in from the periphery (Fig. 69, 4). The remaining nuclei withdraw toward the base, and are separated from the upper part by a septum. The terminal uninucleate cell corresponds to the gametangium of the Mucoraceae, the basal multinucleate cell to the suspensor. The nuclei which do not withdraw into the suspensor at the right time, degenerate. In another less well-known species, *E. pisiformis* (*E. sphagnophila*), copulation is isogamous (in contrast to *E. lactiflua*) and all gametangial nuclei participate in the sexual act, so that, as in the Mucoraceae, many fertilizations occur between the two gametangia, rather than a single gametangial nucleus serving as an asexual nucleus (Atkinson, 1918). Thus both the sporangia and gametangia of *Endogone* seem to be directly connected with the Mucoraceae.

Almost simultaneously with or directly after the formation of the basal septa, the separating walls disappear at the tips of the gametangia and the male nucleus passes over into the female gametangium (Fig. 69, 5 and 6). Near the copulation opening, a thin walled sac grows out on the female gametangium. The contents of both gametangia migrate into this sac which enlarges and becomes a zygospore; its membrane thickens, plugs the basal pore and forms a thick cartilaginous endospore. This apparently corresponds to the cartilaginous layer of the zygospores of the Mucoraceae. Furthermore, numerous verticillate, multiseptate, adherent sheath hyphae surround it (Fig. 69, 7), thicken their walls considerably and form in cross section the so-called halo (Fig. 69, 8). Functionally, this is possibly a substitute for the carbonaceous layer of the Mucoraceous zygospore. In this species, apparently, the nuclei fuse only on germination; in other species, such as *E. pisiformis* (*E. Ludwigii*), fusion occurs shortly after copulation. The germination of the zygospores is unknown. Perhaps it takes place only after the spores have passed through the digestive tracts of animals.

In eleven other mostly northern species, as *E. microcarpa* and *E. macrocarpa*, the zygospores are replaced by similar multinucleate azygospores or chlamydospores (Fig. 68, 6 and 7). In *E. fasciculata*, the chlamydospores arise from a plexus of clearly defined, thick-walled, interlacing hyphae, forming a core from which radiate short, irregular sporiferous branches. Thus the chlamydospores are at first associated in racemose clusters. In the same fructification, the zygospores are formed as a result of homothallic heterogamous conjugation, and are in a scattered group, not in racemose clusters. In the tropical genera, *Sclerocystis* (*Xenomyces*, *Akermannia*) and *Glaziella* (*G. aurantiaca*, *Endogonella borneensis*) the chlamydospores are arranged in special layers within the fructification (Fig. 68, 8 and 9).

The Endogonaceae, especially *E. lactiflua*, show essentially the same characters which we have come to know in the Mucoraceae, only they

are more marked in several respects. In the higher Mucoraceae, *Mortierella*, each single zygospore is surrounded by a sheath; in *Endogone*, numerous sheathed zygospores come together into a fructification with a common ground tissue, thus forming a sporocarp, according to Brefeld's terminology. In *Sclerocystis* and *Glaziella* this fructification shows considerable differentiation. The Mucoraceae, however, are at least morphologically slightly heterogamous, *e.g.*, *Zygorhynchus*, but dynamically still isogamous; some species of *Endogone* are both morphologically and dynamically heterogamous. Thus in the Mucoraceae which have been investigated, the sexual act and fertilization directly follow each other and the gametangia (except *Syncephalis* and its relatives) themselves change to zygospores; in *Endogone*, fertilization is retarded and a dicaryophase, during which the fertilized female gametangium develops into a sac which subsequently becomes a zygospore, is inserted between plasmogamy and caryogamy. This life cycle may be represented as follows:

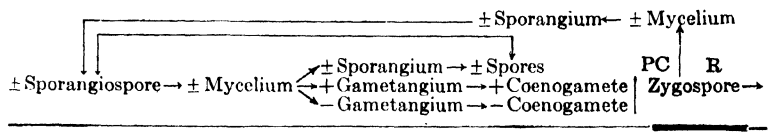


DIAGRAM XII.

This scheme corresponds entirely to that of *Sporodinia grandis* (p. 112), except the formation of the dicaryon, caryogamy and the development of the zygospore is removed one step.

Entomophthoraceae.—This family is mostly parasitic on insects, higher fungi, fern prothalli, etc., rarely saprophytic on orchid seeds and amphibian dung. The thallus is variable, ranging from a well-developed mycelium of the Basidioboleae to the hyphal bodies of the parasitic Entomophthoreae. The sexual reproduction shows a progressive development from the stage represented by *Basidiobolus* where a sporangium, still capable of developing sporangiospores, is discharged, as in *Pilobolus* of the Mucoraceae, to the typical conidium of the higher Mucoraceae which germinates by a germ tube.

The sexual act takes place, as in the Mucoraceae, between coenocytic gametangia, which tend strongly toward heterogamy. The family may be divided into two tribes on the structure of the sexual organs and mycelium: the Basidioboleae with usually uninucleate mycelium and the Entomophthoreae with multinucleate mycelium. In the former, the zygospore membrane is formed as a new structure such as we find in the Ancylistaceae, rather than the usual type of the Zygomycetes.

Basidioboleae.—At present only two species are known in this group, *Basidiobolus ranarum* (*B. lacertae*), saprophytic on the intestinal content and excrement of amphibia (Eidam, 1887; Raciborski, 1896; Fairchild,

1897; Löwenthal, 1903; Woycicki, 1904, 1907, 1927; Olive, 1907; Lakon, 1926; and Levisohn, 1927), and *B. myxophilus* on bacterial zoogloea on fallen pine needles (R. E. Fries, 1899).

The mycelium of *B. ranarum* develops abundantly on the excrement of frogs in 2 to 3 days. It consists of ramose hyphae whose cells when young are uninucleate and sometimes, in age or poor nourishment, multinucleate. The hyphae are persistent in the excrement, but in artificial culture may break up into oidia, resembling the hyphal bodies of the Entomophthoreae.

After a short time, asexual reproduction begins. Each cell grows into a thin, upright sporangiophore, which projects above the medium, swells clavately at its end and absorbs the nucleus and considerable cytoplasm

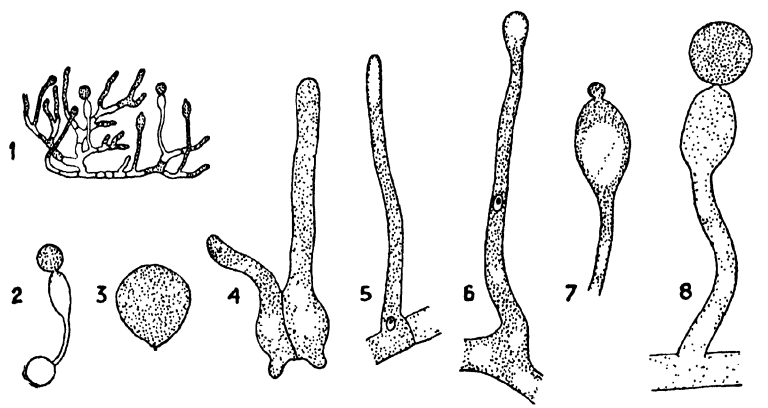


FIG. 70.—*Basidiobolus ranarum*. 1. Young mycelium with conidiophores. 2. Conidium germinating as conidiophore. 3. Conidium. 4. Conidium which has divided once, each half germinating with germ tubes. 5 to 8. Development of conidium and its apparatus of discharge. (1 × 40; 2 × 140; 3, 4 × 375; 5 to 8 × 335; *after Eidam*, 1887.)

from the cell (Fig. 70, 5 to 8). The swelling is abjointed as a sporangium. Although only a thin protoplasmic peripheral layer remains in the sporangiophore, the absorption of water from the mycelium continues uninterruptedly. When the increasing turgidity exceeds the elasticity of the membrane, the sporangiophore splits, and its dome, together with the sporangium, flies off a few centimeters. While still in the air, the portion of the sporangiophore usually falls off the sporangium. The discharged sporangium is pyriform and papillate below (Fig. 70, 3). On the papilla there is a small hyaline peg with triangular base and a small tip with a fine point where the sporangium separated from the sporangiophore.

The sporangia are eaten by beetles, principally Carabidae, Scarabaeidae and Silphidae which prowl about the excrement. These in turn furnish food for the frogs. In the intestinal tract of the frog, the nucleus

of the sporangium divides about three times, forming eight thin-walled sporangiospores, which rupture the sporangial membrane and are liberated. If they are retained for a long time in the intestines of the frog, they may multiply further by ordinary cell division, not by sprouting. When they are excreted they develop the normal mycelium. In artificial cultures, this process may be followed under extremely favorable conditions, but ordinarily the sporangia germinate with one or more germ tubes which soon end in a small secondary sporangium. The sporangia also serve biologically as hypnospores, remaining alive for at least 9 months under laboratory conditions. Their ability to germinate either by sporangiospores or by hyphae is reminiscent of conditions in *Pythium debaryanum* of the Oomycetes.

On the excrement, with failing nourishment, the mycelium begins to form zygospores. Two neighboring cells, or two daughter cells of one mother cell, put forth directly at their septa (in *B. myophilus*) one each

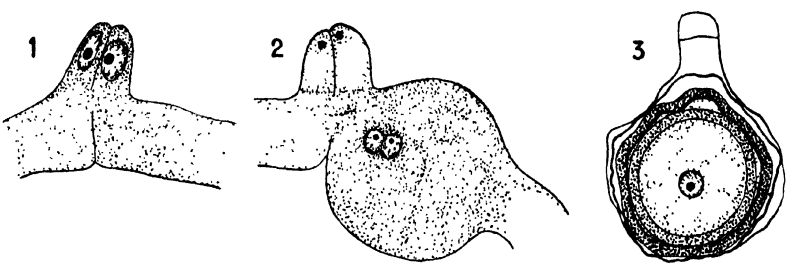


FIG. 71.—*Basidiobolus ranarum*. Development of zygospores. 1. Nuclei resting in the beaks with a pore already formed between the latter. 2. Completed plasmogamy. 3. Mature zygospores. (× 990; *after Fairchild*, 1897.)

above and below, rostrate processes which approach and develop approximately to one-half the cross section of the sporiferous hyphae (Fig. 71, 1). Both nuclei migrate into the beak and divide. Each daughter nucleus, cut off at the tip by a more or less marked septum, degenerates. Both other nuclei migrate basipetally. Meanwhile a pore is formed at the base of the beak; the nucleus of one cell migrates into the other cell, which has swollen in the meantime, and there lies beside the other nucleus (Fig. 71, 2). Under certain conditions, yet insufficiently known, both nuclei of the young zygospore may again divide amitotically, producing four nuclei, of which two degenerate while the other two fuse.

The young zygote withdraws considerable cytoplasm into itself, swells much and surrounds itself with a thin membrane on whose inner side is laid down a thick endospore of several layers (Fig. 71, 3). Generally caryogamy occurs only after two weeks; it may be hastened, however, by desiccation and may then occur after three days; conversely it may be retarded by favorable nourishment. After a rest period, the zygote may

germinate with a germ tube (Fig. 72, 4) which may develop to a mycelium or sporangiophore.

Entomophthoreae.—In this tribe the sporangia have become conidia, as in the higher Mucoraceae. *Conidiobolus utriculosus*, parasitic on Tremellaceae, may be cultivated on artificial media (Brefeld, 1884). Its

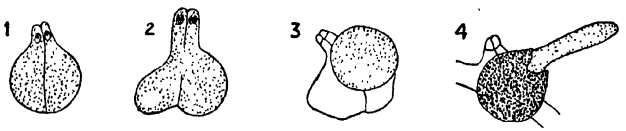


FIG. 72.—*Basidiobolus ranarum.* 1 to 3. A conidium has divided as in Fig. 70 into two halves which behave as gametangia and form a zygospore each. 4. Germinating zygospore. (1 to 3 × 335; 4 × 575; *after Eidam*, 1887.)

conidia germinate with a single germ tube, which in insufficient nourishment, ends in a secondary conidium, but under favorable conditions develops to a mycelium with numerous sacs. This is coenocytic when young; after one or two days, however, it forms numerous septa. Finally

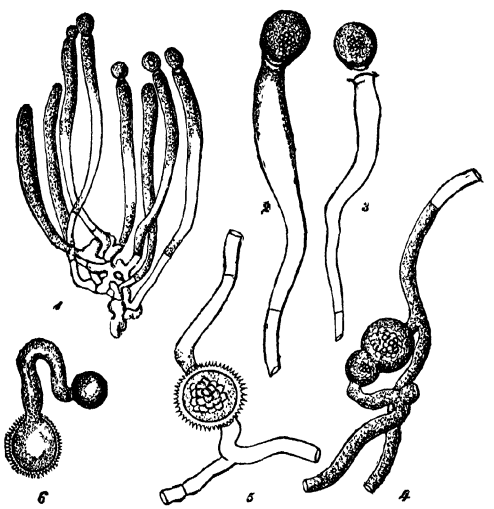


FIG. 73.—*Conidiobolus utriculosus.* 1. Mycelium with condiophores. 2. Single conidiophore. 3. Conidiophore which has discharged its conidium. 4. Copulation of two gametangia. 5. Zygospores. 6. Germination of zygospore with a conidiophore. (1 × 80; 2, 3, 6 × 200; 4, 5 × 150; *after Brefeld.*)

it breaks up and the sacs develop to tubes, each of which grows upward, swells apically and cuts off a conidium (Fig. 73, 1). The septum projects convexly into the conidium. With the further development of the conidium the septum is reversed into the conidiophore and is subsequently differentiated into two lamellae. The conidiophore swells turgidly and

suddenly shoots off the conidium by an arching back of the wall (Fig. 73 2 and 3), which collapses, although uninjured.

The conidiophores and zygospores are formed approximately at the same time. Certain protrusions develop to thick hyphae whose tips swell after contact (Fig. 73, 4). The smaller hypha discharges its content into the larger which is surrounded by a double wall and becomes the hypnospore (Fig. 73, 5). After a few days the zygospore may germinate with one or more hyphae which generally begin to cut off conidia after a short period (Fig. 73, 6). In *Condiobolus villosus*, conidia and asexual hypnospores were produced but no zygospores (Martin, 1925). The cytological relations of this species have not yet been investigated, but in the closely related *Delacroixia coronata*, on agarics and orchid seed, the hyphal cells and conidia are multinucleate (Gallaud, 1905).

The peculiar outgrowths of the mycelium of *Conidiobolus* also appear in *Completoria complens*, parasitic on prothallia and young leaves of several genera of ferns (Leitgeb, 1882). Because its parasitism is limited to a few host cells, its thallus has undergone considerable degeneration, so that in the Entomophthoraceae, *Completoria* occupies a place like that of *Lagenidium* in the Oomycetes. The conidium germinates by a tube which forms numerous protrusions within a host cell, and finally entirely fills this cell which meanwhile has swollen to twice its original volume. Where these protrusions touch the side wall, they penetrate the neighboring cells where they develop to similar knobs. At the end of the vegetative period, the protrusions develop to hyphae, each of which pierces the cell walls and cuts off a conidium. The conidia are discharged by the bursting of the conidiophore. With insufficient nourishment, *e.g.*, in young prothallia, the fungus proceeds to the formation of hypnospores. The content of the group of tubes collects in one or more parts and is surrounded with a thick wall of several layers.

Entomophthora, parasitic on insects, lacks the mycelial protrusions and, in contrast to *Conidiobolus*, increases by sprouting and division; here the sprout mycelium is the only thallus.

Entomophthora Muscae (*Empusa Muscae*) causes epidemics among flies in the fall (Brefeld, 1884; Thaxter, 1888; Olive, 1906). The conidia cling between the hairs of the upper surface of the body. They form a germ tube which generally penetrates the interior through the breathing pores or through the thinner membrane at the junction of the appendages or the thinner parts of the integument on the lower side of the body. Inside it develops into irregular, thick multinucleate fragments of variable form and size, called **hyphal bodies.** These reproduce continually by sprouting and division and are distributed over the whole body by the blood vessels. After 2 or 3 days, the flies are plugged by fungi; they cling somewhere, often on window panes, and die. The hyphal bodies germinate with one or more unbranched germ tubes which

pierce the body wall, especially on the back of the fly and cut off a conidium at each tip (Fig. 74, 1 and 2), into which as many as 18 nuclei enter. Because of considerable water absorption, the conidiophores rupture directly under the septum and discharge the spores with a part of the

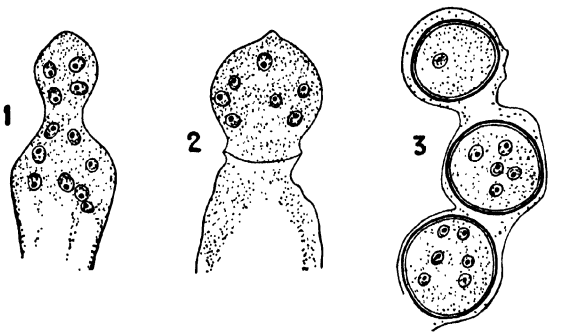


FIG. 74.—*Entomophthora Muscae.* 1, 2. Development of conidiophore. 3. Catenulate gemmae (azygospores?) within old conidiophore. (1, 2 × 720; 3 × 800; *after Olive*, 1906, *Goldstein*, 1923.)

protoplasm so that the flies are surrounded by a ring of spores. In old, dried-up flies, the hypnospores arise in masses as thick-walled, multinucleate, intercalary swellings of the hyphae (Fig. 71, 3). Whether they should be regarded as gemmae or azygospores is still obscure (Goldstein, 1923).

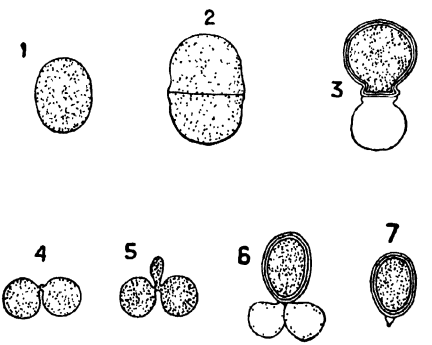


FIG. 75.—*Entomophthora Grylli.* 1 to 3. Development of zygospore from hyphal body. *Entomophthora Fresenii.* 4 to 7. Development of zygospore from two hyphal bodies. (1 to 3 × 145; 4 to 7 × 290; *after Thaxter*, 1888.)

The other species of *Entomophthora* show essentially the same characters as *E. Muscae.* For hypnospores they form both zygospores and azygospores. In *E. Fresenii*, two hyphal bodies change into gametangia and copulate (Fig. 75, 4 and 7), whereby the junction swells to a zygospore

(Thaxter, 1888). In *E. Grylli* the hyphal bodies divide by a septum into two daughter cells; hereupon the content of one passes over into the content of the other (Fig. 75, 1 to 3) and this becomes a zygospore (Thaxter, 1888). In this species azygospores may be formed instead of zygospores; under favorable conditions the hyphal bodies put forth a process which takes up the protoplasm together with the nuclei, is abjointed and surrounded with a thick wall. The nuclei neither divide nor fuse. Accordingly the azygospores develop entirely parthenogenetically (Riddle, 1907).

The remaining species are distinguished by uninucleate conidia and branching conidiophores, as *E. sphaerosperma* (*E. radicans*) on the caterpillars of cabbage butterflies (Brefeld, 1881), *E. Sciarae* on the larvae and imago of *Sciara*, a small species of fly (Olive, 1906), *E. geometralis* on a moth (Riddle, 1907), *E. americana* on certain flies (Riddle, 1907), *E. Delpiniana* (Cavara, 1899) on *Polyete lardaria*, etc. The germ tube rapidly penetrates the host, especially the fat bodies, branches, and forms a coenocytic mycelium with only a few septa (Fig. 76, 1). When the fat body is consumed and the hyphae have reached the blood vessels, they divide (in some species, *e.g. E. sphaerosperma*) into hyphal bodies which increase by sprouting and division. Under certain conditions these may be changed to gemmae by the thickening of their walls. After approximately a week, the infected insects die. The whole content, even to the tracheae and stomach contents, is used up and the insects are changed into mummies (fungus pseudomorphs). Toward the end of this time, in the species with undivided mycelium, *e.g.*, *E. Delpiniana*, the number of septa increases considerably, and the hyphae are eventually divided into cells with few nuclei. These (in other species corresponding to the hyphal bodies) develop almost simultaneously to long tubes which pierce the body wall on all sides. On the lower side of the insect they change to rhizoids and attach the dead body to the substrate. On the distal side they develop conidiophores and fork so much that the branches form a palisade and surround the insect with a thick felt. Some of these threads remain sterile and become setaceous, like the paraphyses of the hymenium in the higher fungi. The others form at each end a young conidium into which a nucleus (in *E. Culicis* 2) slips and which is finally cut off by constriction. They swell by continual water absorption and discharge the conidia for a considerable distance as the Piloboleae do their sporangia. The thin-walled conidia retain their ability to germinate for about 8 days; under unfavorable conditions each germ tube ends with a secondary conidium.

At the appearance of unsuitable growth conditions, hypnospores, zygospores and azygospores are formed. In *E. sphaerosperma*, only azygospores are known. As the season progresses the hyphal cells no longer develop conidiophores but their content migrates into a pro-

tuberance which is abjointed. The empty hyphal cells break up so that the mummy seems to be filled only by resting spores. In *E. Culicis* and *E. Delpiniana*, the azygospores, like the conidia, arise as terminal swellings of the hyphae (Fig. 76, 3 and 4) and then surround themselves with double walls.

In other species true zygospores are formed. In *E. americana* and *E. geometralis*, two species with hyphal bodies arise in two different ways

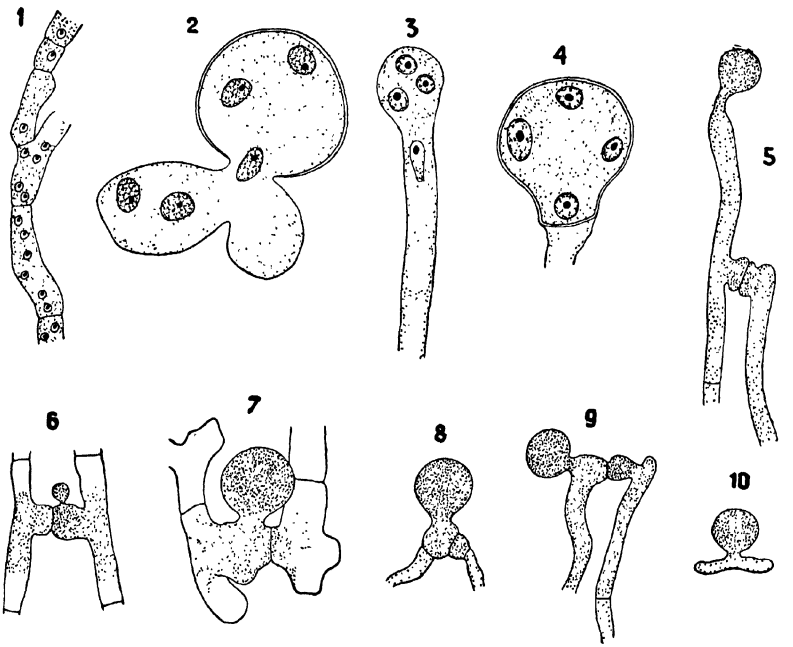


FIG. 76.—*Entomophthora Sciarae*. 1. Young hypha. *Entomophthora americana*. 2. Two gametangia fused at the tip, forming a lateral zygospore. *Entomophthora Culicis*. 3, 4. Development of an azygospore. *Entomophthora echinospora*. 5. Copulation. *Entomophthora sepulchralis*. 6, 7. Development of a zygote. *Entomophthora occidentalis*. 8, 9. Copulation; the zygote develops from one gametangium at a distance from the point of copulation. *Entomophthora sphaerosperma*. 10. Development of an azygospore. (1 × 180; 2 × 500; 3, 4 × 720; 5, 8 to 10 × 290; 6, 7 × 145; *after Olive*, 1906; *Riddle*, 1907, *and Thaxter*, 1888.)

(Riddle, 1907). In one case, hyphal bodies fuse near their tip and the zygospore buds, as in *Piptocephalis* (Fig. 63), laterally from the point of fusion (Fig. 76, 2). In the other case, copulation takes place, as in *E. Fresenii*, through an H-formed piece, whereby the zygospores, as in *Syncephalis*, are far removed from the point of fusion out of which a gametangium grows. Caryogamy occurs only on germination. Similar relationships are shown by *E. occidentalis* and *E. echinospora* (Thaxter, 1888), which do not break up into hyphal bodies but in which copulation

(in the latter extramatrical) takes place between hyphal ends (Fig. 76, 5, 8, 9). In *E. sepulcralis* within or without the host, two hyphae form lateral outgrowths which often dissolve the separating wall without abjunction from the hyphae. The zygote does not arise at the point of fusion but on a copulation branch (Fig. 76, 6 and 7). *E. rhizospora* forms its zygospores extramatrically like *E. echinospora;* in it the remaining extramatrical hyphae become sclerotia and without being dissolved change into a horny, chocolate-colored tissue which holds the spores firmly together (Fig. 77).

In many Entomophthoreae only hypnospores are known. These are provisionally placed in *Tarichium* (Lakon, 1915).

The relation to the other Zygomycetes, especially the Mucoraceae, is still obscure. As regards their asexual fructification they appear

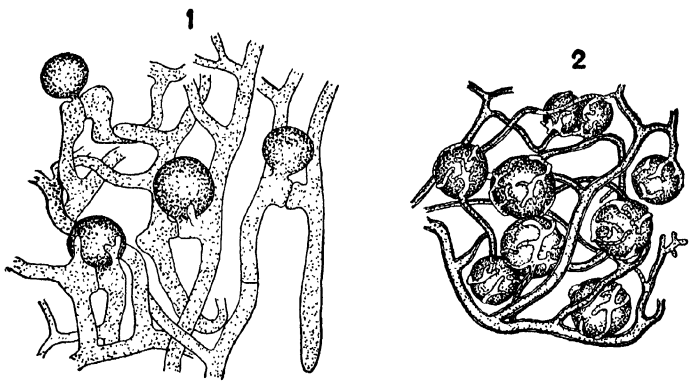


FIG. 77.—*Entomophthora rhizospora.* 1. Group of extramatrical hyphae, forming zygospores. 2. Old hardened hyphae which surround the zygospores with rhizoidal processes. (× 290; *after Thaxter,* 1888.)

below these as they possess no conidiophores but only conidial hyphae. As regards their sexual fructification, however, they are on the same level. Possibly we have to do with two parallel unrelated lines.

Summary.—The thallus develops from a uninucleate, centrally organized thallus to a multinucleate, eventually septate, mycelium whose hyphae are adapted to independent existence. The organs of reproduction, sporangia and gametangia, however, remain essentially the same in their gross characters. In comparison with the thallus, they require a continually smaller supply of material and hence one individual can form increasingly larger numbers. By a premature end of development, the individualization of the daughter cells is suppressed; the sporangia become conidia, and their daughter cells assume the task of propagation; the gametangia remain equally coenocytic, a continually decreasing number of their nuclei function as sexual nuclei, and they

assume the function of sexual cells, instead of gametes. Thereby arises the possibility of the transition from hydrochory to anemochory, and from hydrophily to gametangial copulation, *i.e.*, from aquatic to terrestrial habitats. Plasmogamy and caryogamy are separated in time and place, and the diplophase is lengthened by the insertion of a short dicaryophase beyond the true zygote. The zygotes become increasingly specialized as hypnospores and finally co lect in conspicuous fructifications.

CHAPTER X

ASCOMYCETES

The Ascomycetes are those fungi in which meiosis takes place in characteristic sporangia with endogenous spore formation. These sporangia are called asci, their spores, ascospores.

Their thallus is generally well developed and much branched; its hyphae (in contrast to those of the Phycomycetes) are regularly divided by septa into uni- or multinucleate cells. Under certain conditions of nourishment, they may continue growth by sprouting; in some forms, only sprout mycelium is known.

The imperfect forms reach the culmination of development in this group. Besides oidia, gemmae, etc. the most varied conidia are produced. Sometimes they are borne in stromata, pycnidia, etc.; at times these fructifications approach the perfect forms in size and luxuriance of growth. In certain families, several of the imperfect forms may appear successively or simultaneously on the same species (polymorphism). In case the corresponding perfect form is unknown, the imperfect forms are classified as Fungi Imperfecti and given special names; for practical reasons these are occasionally retained in plant pathology, even when the corresponding ascus form has been discovered, as often only the imperfect forms are encountered (see Chapter XXXV).

The sexual organs in a way suggest those of the Zygomycetes and, like them, are formed as simple isogamous or heterogamous copulation branches. In the higher forms, they undergo an extensive functional and morphological differentiation: the male copulation branch becomes an antheridium and the female an ascogonium. The antheridia generally exceed only by little the original size of the copulation branch, and at most they coil helically. The ascogonia undergo specific further development and in addition retain (or initiate) trichogynes; this corresponds functionally *mutatis mutandis* to the fertilization tubes of the Oomycetes. In the simplest case, the sexual organs are arranged as shown in Fig. 78: a unicellular antheridium approaches an also unicellular ascogonium and is surrounded by a trichogyne; thereby ascogonium and trichogyne form the female copulation branch.

Subsequently both the ascogonia and trichogynes may become multicellular and coil characteristically and furthermore the ascogonia may be borne on stipe cells; thereby arises a typical structure which earlier was designated as Woronin's hypha, or scolecite.

Because of a peculiar weakening of sexual tendencies in the Ascomycetes, plasmogamy early loses its obligatory character and becomes facultative. This functional disturbance first affects morphologically only the antheridia: these become superfluous and disappear, and instead of amphimictic fertilization, appear all sorts of deuterogamous processes which we shall later follow in detail under the individual orders. Gradu-

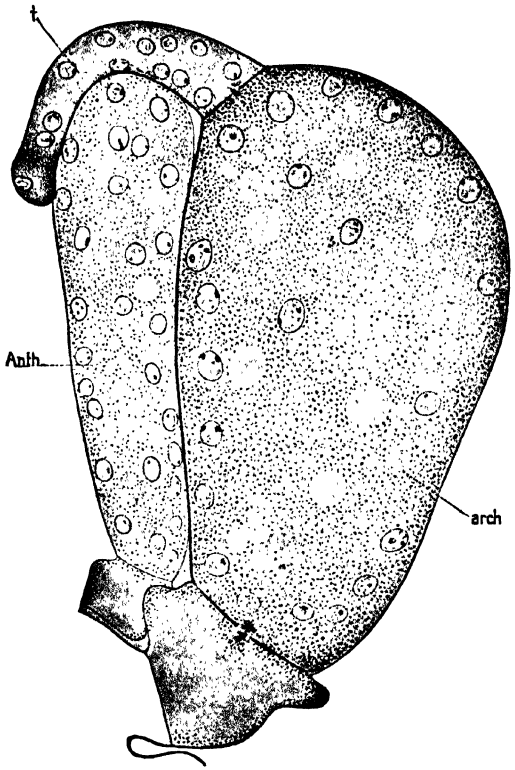


FIG. 78.—*Pyronema confluens*. Sexual organs. Antheridium, *Anth*, and ascogonium, *arch*, with trichogyne, *t*. (× 1,750; *after Claussen*, 1912.)

ally, however, this functional degeneration extends to the female organs; they also degenerate and disappear. Eventually no organ is formed and the plasmogamy becomes pseudogamous.

Hand in hand with this degeneration, there also appears a shifting of the significance of the sexual organs for the formation of fructifications. Originally the laying down of the fructifications was begun by the formation of sexual organs; hence the female organ was called archicarp. In many higher forms, the fructifications begin their development inde-

pendent of the sexual organs, by the physiological stimulation of nourishment, and the sexual organs are later formed in them.

As was the case in the Endogonaceae, so also in the Ascomycetes, plasmogamy is not followed directly by caryogamy but one or several dicaryons are formed (according to the number of gametangial nuclei). In the lower forms the dicaryon migrates directly into an ascus (as into the zygote of *Endogone*) which is formed as the product of the plasmogamy. In the higher forms, caryogamy is more and more retarded and the fertilized gametangium develops into one or more hyphae which take up the dicaryon and, by conjugate division, branch and proceed to the formation of asci. These dicaryotic hyphae are called **ascogenous**

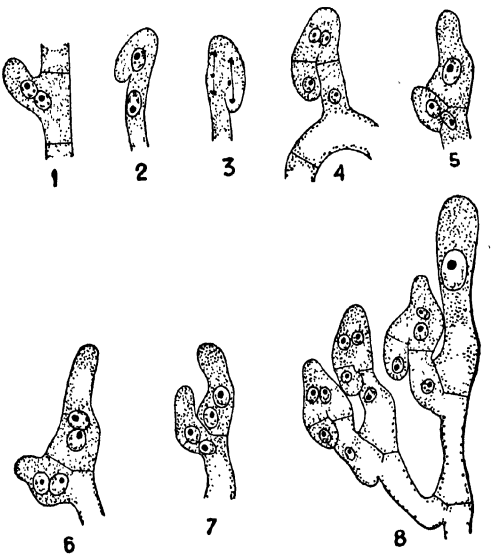


FIG. 79.—*Pyronema confluens*. Development of ascogenous hyphae. (× 1,165; *after Claussen*, 1912.)

hyphae; biologically they offer the advantage that, in contrast to the lower forms, one gametangium can create a number of asci.

In most of the higher Ascomycetes, the asci arise on the ascogenous hyphae according to the hook type. In this connection may be mentioned *Pyronema confluens*. The ascogenous hyphae springing from the ascogonium are coenocytic, *i.e.*, they contain a number of dicaryons (Fig. 221, 1), and develop by repeated forking, more or less vertically toward the top of the future fructification. Subsequently they divide by septa so that in the neighborhood of the ascogonium, the cells contain 2 to 8 dicaryons and farther away only one (Fig. 221, 2). A cell with only one dicaryon puts forth a lateral process whereby the nuclei become

rather far separated; shortly the process bends around into a hook (Fig. 79, 2) and the nuclei begin to divide conjugately and to draw into a layer (Fig. 79, 3). The spindles lie approximately parallel to each other. After the division, the crook is abjointed from both the tip and the stipe (Fig. 79, 4); thus the crook contains two nuclei, while the tip and stipe contain one nucleus each. In the simplest case, the nuclei of the crook fuse to a diploid nucleus, the primary ascus nucleus (Fig. 79, 5), and the crook develops to an ascus. In another case, the crook develops to a new hook, which again develops, etc., so that several lie transitorially behind one another (Fig. 79, 6 to 8); only the last terminal hooks proceed to ascus formation. In the third case, the dicaryon of the hook divides without a previous formation of a new hook. The crook develops a branch which only later returns to hook formation; on these hooks, asci may arise directly; or caryogamy may be again displaced, so that a tuft of hooks arises (Fig. 79, 8). By the combination of these various possi-



FIG. 80.—*Geopyxis catinus*. Development of ascogenous hyphae. (*After Guillermond*, 1905.)

bilities there have arisen those manifold pictures which have so long delayed the morphological comprehension of ascogenous hyphae. Occasionally hook stipe and hook tip fuse, the stipe nucleus generally migrating into the tip (Fig. 79, 5 and 6); the tip cell which has now become binucleate develops a branch which gradually forms a hook; this hook can, by fusion of its nuclei, develop directly to an ascus or again (Fig. 79, 8) grow into a transitory tuft of hooks.

Besides the characteristic formation of hooks, the ascogenous hyphae of *Pyronema confluens* pass through two morphologically different phases of development. In the first phase (directly after development from ascogonia), they are coenocytic and longitudinally striate and develop with normal growth of the tip; in the second phase (after the growth from septate hyphae), they only develop further by hook formation and have only one dicaryon in each cell. The most striking development of primary and secondary ascogenous hyphae, we meet in the Plectascales.

In addition to the hook type, a whole series of other developmental forms of ascogenous hyphae is known in the higher Ascomycetes. In

Geopyxis catinus (*Peziza catinus*), the terminal cell of the ascogenous hypha (like the hook cell of *Pyronema confluens*) is uninucleate, the subterminal is binucleate (Fig. 80). This subterminal cell grows out laterally and develops to an ascus (Guillermond, 1905*a*).

Somewhat further removed is the *Plicaria* (*Galactinia*) type, (Maire, 1905) which includes *Plicaria succosa* (*Galactinia succosa*) and *Acetabula leucomelas* (*Peziza leucomelas*). In these, the ends of the ascogenous hyphae include a series of cells with a dicaryon each, the terminal cell of which develops to an ascus by the fusion of its nuclei. This type, however, in spite of its morphological picture, which is entirely at variance with the *Pyronema* type (as also the systematic relationships of all these forms would allow us to suppose), does not seem to be fundamentally different. As an anomaly in *Pustularia vesiculosa* (*Peziza vesiculosa*), the ascogenous hyphae may form a hook of the *Pyronema* type, whose crook cell, instead of developing to an ascus by repeated division of its dicaryon, grows into an elongate hypha whose terminal cell proceeds to the formation of an ascus according to the *Plicaria* type.

Still further removed from the hook type, is a fourth which has not yet been investigated cytologically. In it the cells of the ascogenous hypha, as in the *Plicaria* type, apparently each contain a dicaryon. A large number of them, however, develop asci (in contrast to the *Plicaria* type) so that the asci lie behind each other, as in a chain, and then divide. Possibly this type is the most primitive of the four, as it has only been definitely ascertained in the lower Plectascales. It has been named by Dangeard (1907) the rectascous type in contrast to the curvascous type of *Pyronema*.

In a fifth type, finally, no true ascogenous hyphae are formed, but asci develop from a cell complex which arise directly from the fertilized cells of the ascogonium. We will discuss this type more fully in the Laboulbeniales.

The further development of the asci, as far as is known, is the same in all Ascomycetes. The primary ascus nucleus, which has arisen from the fusion of the dicaryon, undergoes three steps in division with meiosis, whereupon the eight daughter nuclei cut out eight ascospores from the cytoplasm of the ascus by free cell formation. The cytoplasm remaining behind is called **epiplasm**; in addition to the nourishment of the ascospores growing in it, it provides for the formation of the sculpturing of the spore walls. In certain forms, the number of divisions may be limited to two or rise to sixteen, whereupon in the first case the number of nuclei is reduced to four, in the second rises to many thousand (64,936). In case the ascospores are thick walled, they possess a typical terminal germ pore or a meridional slit; in the latter case the two halves of the ascospore wall separate in germination like the cover of a box. According to the Anglo-Saxon school (especially represented by Harper and Gwynne-

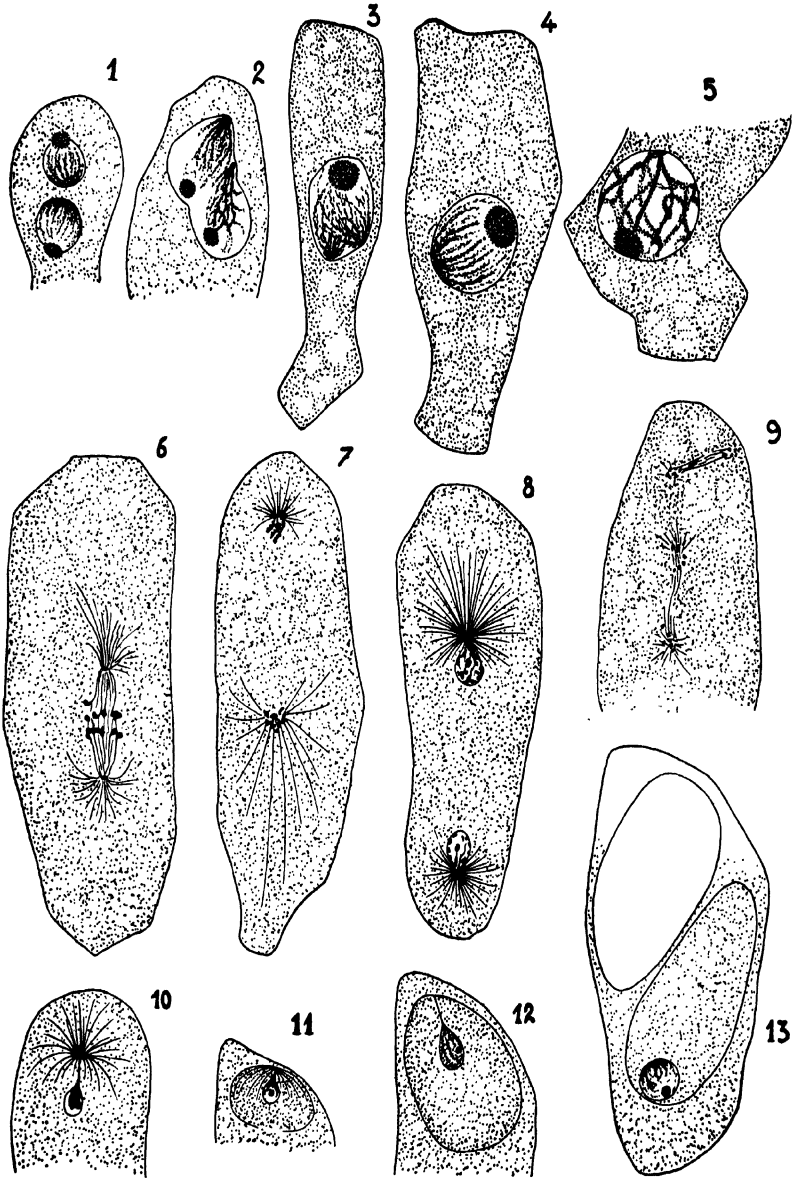


FIG. 81.—*Phyllactinia corylea*. 1. Young ascus with dicaryon. 2 to 4. Caryogamy. 5. Spireme. 6 to 9. Steps in division of primary ascus nucleus. *Erysiphe cichoracearum*. 10 to 12. Spore formation. 13. Immature ascus. (1 to 5 × 1,500; 6, 13 × 1,000; 7 to 12 × 670; *after Harper*, 1905.)

Vaughan (née Fraser) the nuclear fusion in the young ascus is not the first and only fusion, but is preceded by another fusion in the ascogonium directly after the sexual act. The ascogenous hyphae, according to this conception, do not contain haploid dicaryons but undivided diploid nuclei which only after the formation of the hooks, come together to dicaryons. Because of this double fertilization, this primary ascus nucleus is tetraploid, and, according to this school, contains $2x$ double chromosomes. In the first step in division (heterotypic division or meiosis) each daughter nucleus contains $2x$ simple chromosomes. The second step is homoeotypic, the $2x$ simple chromosomes are halved so that every daughter nucleus still contains $2x$ simple chromosomes. In the third step (**brachymeiosis**) one-half the undivided chromosomes migrate to each pole, so that the daughter nuclei of the third generation contain x simple chromosomes. Although the cytological findings in part contradict each other (Guillermond, 1913) *e.g.* Claussen (1912) states the haploid number is 12 while his figures never show more than 6 (Tandy, 1927)—and in part may be interpreted to either conception, at present the author prefers the theory of simple fertilization as developed by Dangeard (1907) and Claussen (1912). According to this conception, the life cycle of the Ascomycetes in the ideal case proceeds according to the following scheme:

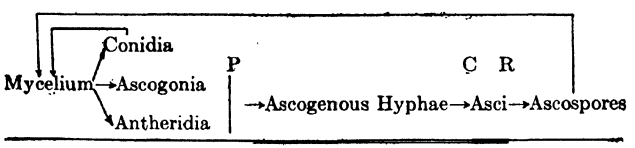


DIAGRAM XIII.

There arise on the haplont, first imperfect forms, then sexual organs (antheridia and ascogonia). Between these sexual organs plasmogamy takes place, whereby each male and female nucleus pair as a dicaryon. These dicaryons migrate into the ascogenous hyphae and divide conjugately. The ascogenous hypha, thus, caryologically represents a special phase of the diploid phase, the so-called dicaryophase; to be sure, this is virtually diploid; cytologically it only produces dicaryons from two sexually different haploid nuclei.

The dicaryophase, and with it the sexual process altogether, ends with nuclear fusion in the young asci (caryogamy). Caryogamy is followed directly by meiosis, usually producing eight haploid ascospores.

In the higher Ascomycetes, this scheme of development is further complicated, since the haploid thallus proceeds to form fructifications on or in which the ascogenous hyphae complete their development. As in most Florideae and in the sporophyte of the mosses, the dicaryophyte is to a certain extent parasitic on the haplont and nourished by it.

In the simplest case, these fructifications form an undifferentiated mass of tissue, a stroma, on or in which the asci are formed. A fructification of this sort is called ascostroma or ascoma; it corresponds approximately to the sporodochium and acervulus of the fructifications of the imperfect forms.

In the higher forms, the hyphal tissue of the stroma undergoes many differentiations both in form and histological structure, and develops to fructifications which form the basis for the systematic classification of the Ascomycetes. All these higher fructifications are referred to two basic forms, perithecium and apothecium.

The **perithecia** (Fig. 82) consist of a solid, often pseudoparenchymatous, wall and a cavity containing the asci. The more primitive types are usually spherical; the asci lie irregularly in the interior and are only liberated at the decay of the perithecial wall; thus the lower forms are **cleistocarpous.** In the higher types, they are generally flask shaped; at their top, there is formed by the periclinal arrangement of the hyphal elements during the course of development, a special opening (**ostiole**) whose canal is often closely covered with hyphal ends, **periphyses** (Fig. 82, *e*). Between the asci (generally basal), there are arranged sterile, haploid, hyphal branches, the **paraphyses,** which serve chiefly to nourish the growing asci. While young they are rich in reserve materials; during development of the fructification they become vacuolate and in some forms finally disappear.

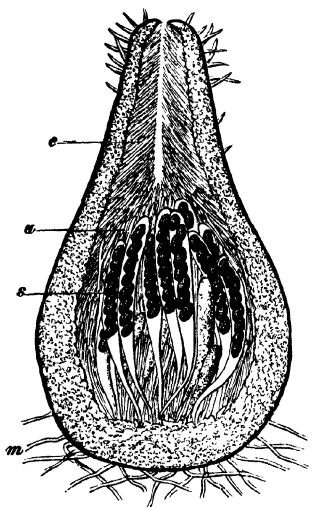


FIG. 82.—*Podospora fimiseda.* Perithecium. *e*, periphyses; *a*, asci; *s*, ascospores; *m*, hyphae. (*After Tavel*, 1892.)

The liberation of the ascospores from these flask-shaped perithecia takes place in various ways. In many forms, they are liberated into the interior of the perithecium by the disintegration of the asci and are then gradually pushed out. In other forms, they are actively shot out. A good example was described by Zopf (1883), for two relatives of *Podospora fimiseda* (*Pleurage fimiseda*) shown here, *P. minuta* and *P. curvula*, which, because of their transparent perithecia, allow one to follow under the microscope the course of spore discharge in the unaltered living perithecium. The asci are cylindrical and at the beginning of the discharge period their upper third broadens. Hereupon one ascus after another elongates, penetrates the opening of the perithecium and projects above the ostiole. Then it bursts and shoots off its top, with ascospores firmly attached to it and to

each other by a gelatinous appendage. The rest of the ascus collapses, withdraws and makes place for the next. The height of projection of the ascospores occasionally attains a relatively enormous value if one considers that the perithecia are only about half a millimeter high in the middle. Thus in *Podospora fimiseda*, it reaches 15 cm. and in *P. curvicolla*, as high as 45 cm. (Weimer, 1920).

In other forms, as *Leptosphaeria acuta* (Hodgetts, 1917), *Pleospora herbarum* (Atanasoff, 1919) and *P. scirpicola* (Pringsheim, 1858), this discharge is favored by an anatomical differentiation of the ascus wall. This consists of two layers which are only recognizable at the moment of spore liberation, a rigid inelastic cuticular outer layer which does not swell in water, and a thicker gelatinous inner which absorbs water and swells. The paraphyses also swell in damp weather. By the pressure of the swollen inner layer, the outer ruptures at the tip, the inner together with the ascospores pushes out, tears open laterally with a jerk at the point of emergence or at the top and discharges the ascospores.

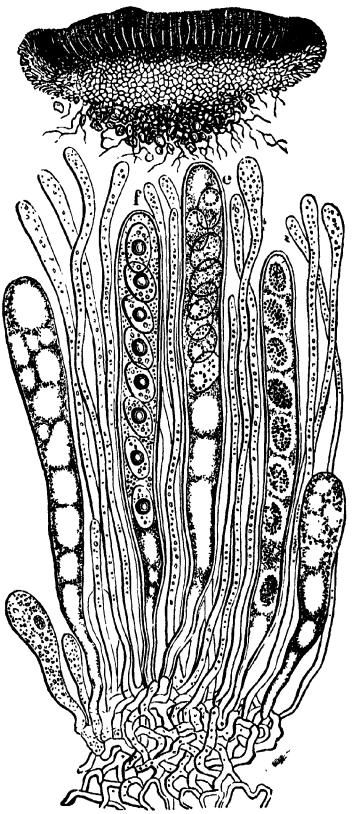


FIG. 83. — *Humaria convexula*. Above, cross section of apothecium. (× 20.) Below, section of hymenium showing asci and paraphyses. (× 550; *after Sachs*.)

In still other forms, as in *Endothia parasitica* and in many Gnomoniaceae, the length of the perithecial neck does not permit the asci, as in *Podospora*, to reach the opening and there to eject their spores. Hence they break loose from their point of formation and closely press together, more or less parallel, with the tip, directed toward the entrance canal and fill up the interior of the perithecium. Hereupon they are gradually pressed out through the canal by the periphyses. On the drying of the perithecial neck, the asci are pressed together until they rupture under the lateral pressure and discharge their spores. Thus the mechanism of discharge here rests in the perithecial opening; if this is cut off, at least in *Endothia parasitica*, spore discharge ceases (Heald and Walton, 1914).

The **apothecium,** the second basic form mentioned above, differs from the perithecium mainly in the greater development of the fertile

part (Fig. 83); consequently the asci are united into a broad continuous layer, a hymenium, which in certain forms, especially lichens, can occasionally continue its growth for years. By this lateral development of the fertile part, the top of the fructification is ruptured into shreds, so that at maturity the hymenium is exposed. As with the perithecia, the asci in the apothecia are generally imbedded between paraphyses (Fig. 83); at times, as in certain Geoglossaceae, these arise in special rich storage cells similar to the auxiliary cells of the Florideae and hence show their primary function as nutritive organs.

Corresponding to the open position of the mature asci, the violence of ascospore discharge has undergone a considerable increase. In several groups, the top of the ascus opens like a cover whereupon the ascospores are shot out with great force (in *Ascobolus immersus* up to 35 cm. high), and, as in the perithecia, are given over to an anemochoric dissemination. As in the discharging perithecia, so also in the discharging apothecia, all spores of one ascus remain clinging together by gelatinous shreds or sheaths, so that an enlargement of the discharged mass is attained; thus the volume of one of these spore balls of *Ascobolus immersus* is about 2,000 times larger than that of a basidiospore (Buller, 1909); thus may easily be explained the greater momentum with which these fungus "cannons" shoot off their projectiles. As in many discharging perithecia, *e.g.*, those of *Endothia*, so also in many discharging apothecia, the activity of the asci is largely dependent on external influences (Falck, 1916); still others react chiefly to mechanical stimuli, as those which are liberated by currents of air or wind (Falck, 1923).

Systematic classification of the Ascomycetes rests upon the degree of development of the dicaryophase. Those forms in which the dicaryophase is lacking and in which the sexual cells and ascus arises directly as the product of a sexual act are called Hemiascomycetes; those forms in which the sexual organs (*Thelebolus* and the Laboulbeniales excepted) developed to ascogenous hyphae which in turn are adapted to the formation of numerous asci are called the Euascomycetes or typical ascomycetes. We will discuss briefly, in the review at the close of the Ascomycetes, the probable phylogeny of these two subclasses and the phylogenetic derivation of the Ascomycetes as a whole, when the reader will have oriented himself in the various forms.

CHAPTER XI

HEMIASCOMYCETES

The Hemiascomycetes form the link between the Ascomycetes and the Phycomycetes. According to the classification followed here they fall into two orders, Endomycetales (Saccharomycetales) and Taphrinales (Exoascales). The Endomycetales include those forms in which an ascus arises directly as product of the sexual act (wherever this takes place). They resemble the Zygomycetes, as will appear in the following discussion, only, instead of the zygospore, an ascus develops as a hypnospore. The Taphrinales include two isolated, incompletely investigated families which have some primitive characters in the development of their asci, without any closely related forms in the Ascomycetes known at present.

ENDOMYCETALES

The Endomycetales are divided into three families: the Dipodascaceae, the Endomycetaceae and the Saccharomycetaceae. In the Dipodascaceae, a multispored ascus arises from the copulation of coenocytic gametangia. In the Endomycetaceae, the gametangia (wherever they are formed) are uninucleate at the time of copulation; each zygote develops to a typical ascus of eight or fewer spores. In the Saccharomycetaceae, gametangial copulation is replaced by a pseudogamy whose product (if it really is completed) is a typical ascus of not more than eight spores, as in the Endomycetaceae. Both the Endomycetaceae and Saccharomycetaceae develop rapidly to apomictic forms.

Dipodascaceae.—The only known representative of the family, *Dipodascus albidus*, was originally found in the slime-flux of a bromeliad in Ecuador, later in the same habitat on birch in Sweden. The hyphae are branched, septate, divided into multinucleate cells of variable length. In nutritive solution, they break up into oidia. Under unfavorable conditions, they form gemmae: their content rounds off and surrounds itself with a thick membrane.

After a few days, two neighboring cells put forth young copulation branches directly beside the septum separating them (Fig. 84, 1). At first both copulation branches are of the same size and it is impossible to determine which will later be the male and which the female. Frequently the female branch appears somewhat earlier and survives through the whole development of the male. Occasionally both copulation branches may arise from different hyphae (Lagerheim, 1892; Juel, 1902; 1921;

Dangeard, 1907). When the copulation branches have attained a certain length, their tips come in contact, whereupon they abjoint from

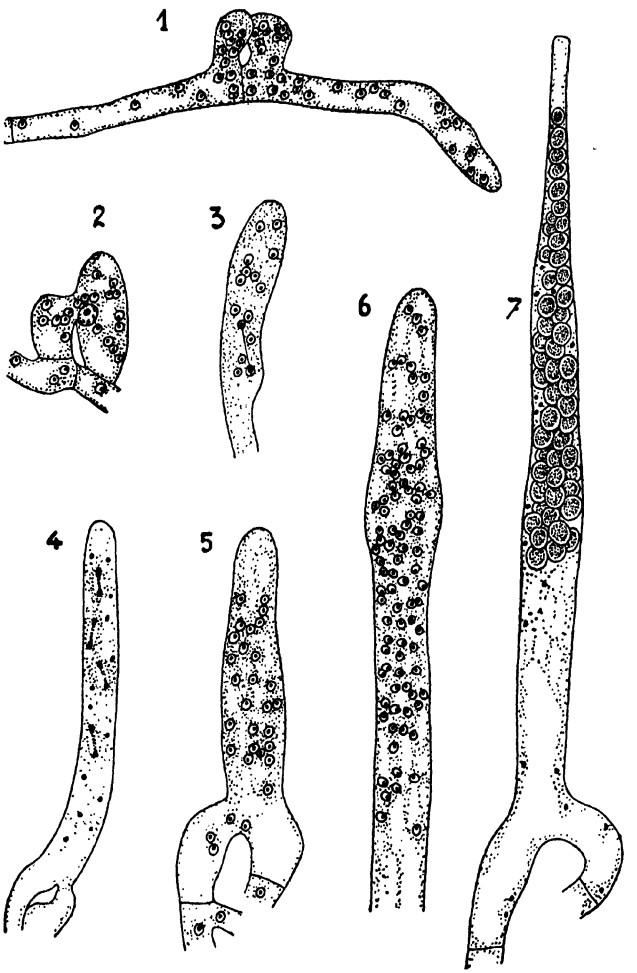


FIG. 84.—*Dipodascus albidus*. 1. Young copulation branches not yet abjointed. 2. Diploid nucleus in female copulation branch. 3. First step in division of diploid nucleus. 4. Telophase of 3. 5, 6. Later stages of young ascus. 7. Nearly mature ascus, the dark points indicating degenerate nuclei. (1, 2, 5 to 7 × 900; 3 × 800; 4 × 600; *after Juel*, 1902 and 1921; *Dangeard*, 1907.)

the sporiferous hypha, an apical gametangium of 10 to 12 nuclei; generally the septum lies near the hypha, but it may be shifted rather far toward the top, in which case the gametangia rest on suspensor-like stipes.

When the septum between two gametangia is dissolved, a sexual difference between the copulation branches begins to appear. Nuclei of the male gametangium migrate into the female, whereby a male and a female nucleus fuse in the gametangium near the copulation canal (Fig. 84, 2). The female gametangium develops an elongate tapering ascus at the tip, while the male ceases development. The fusion nucleus which was originally very large, undergoes several successive divisions whereby the daughter nuclei gradually approach in size and appearance the supernumerary original gametangial nuclei and finally may not be distinguished from them (Fig. 84, 3 to 6). Each cuts out of the cytoplasm a large, thick-walled ascospore while the non-functional gametangial nuclei gradually degenerate (Fig. 84, 7). At maturity, the ascus opens at the tip. The spores, with the rest of the protoplasm, are forced out and collect before the opening as a slimy, sticky ball. They are capable of immediate germination. As an exception, this development may take place parthenogenetically where the gametangia develop asci without fusion.

The fertilization of *Dipodascus* is strikingly reminiscent of that of *Endogone*. As in the latter, only one gametangial nucleus is activated as a sexual nucleus; only, at least in *Endogone pisiformis*, the supernumerary unprivileged nuclei are pushed out of the gametangium, while in *Dipodascus* they remain in the gametangium and only are resorbed in the development of the ascus. Furthermore, the product of the sexual act is a thick-walled hypnospore in *Endogone* while it is a sporangium in *Dipodascus*. These differences may be explained, however, by the different biological conditions of the two genera. Even the free cell formation of *Dipodascus* can cause no difficulty in the conception. If the content of the asci were divided by cleavage, as is always the case in the sporangium of *Endogone* and other Zygomycetes, the unactivated gametangial nuclei would survive in the spore. That can only be avoided if each daughter nucleus of the fusion nucleus forms a membrane within its sphere and leaves the unused protoplasm with the original vegetative nuclei as periplasm. Hence it appears justifiable to seek the roots of the Dipodascaceae in the Zygomycetes with a life cycle of the type of *Endogone*.

Endomycetaceae.—This family is often saprophytic on sugar containing substrates, in the slime-flux of trees, the ambrosia fungi in the borings of Coleoptera, more rarely parasitic in fructifications of Agaricaceae and on man. Some of the species are used in Asia and Africa by the natives as yeasts for fermentation. The best-known representatives are *Eremascus* and *Endomyces*. In the former were originally placed the sexual, in the latter the asexual forms; more recent investigations have entirely destroyed these differences.

As a starting point *Eremascus fertilis* on fruit juices (Stoppel, 1907; Guillermond, 1909) should be mentioned. The hyphae are often branched

and consist of long, narrow cells which are multinucleate (up to 15) in the neighborhood of the growing tip (Fig. 85, 1). In the older part, however, they are uninucleate by septation. Approximately 5 days after sowing in artificial culture, two cells form copulation branches in the region of their septa (Fig. 85, 2). The copulation branches do not always arise simultaneously, however, and their length is often unequal; also, both processes may not arise from neighboring cells but from cells separated by a small, intermediate sterile cell. If they are not too short, they make a half to complete turn about each other. In *Eremascus albus* (Eidam, 1883*a*), they coil helically (Fig. 86).

Their tips touch, the walls at the point of contact are dissolved, and the two copulation branches come into open communication. The

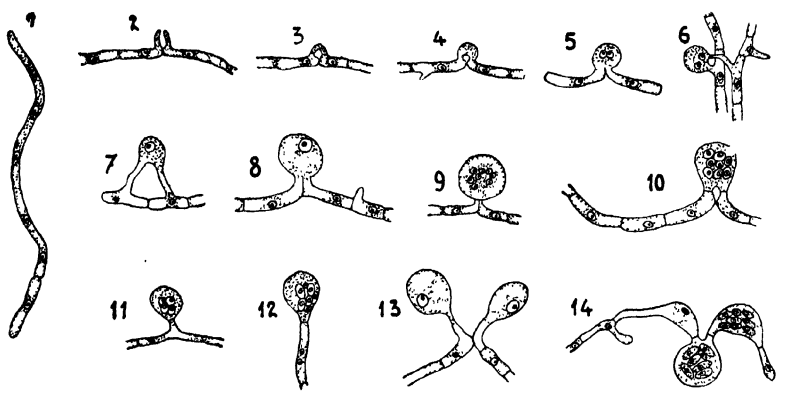


FIG. 85.—*Eremascus fertilis.* Development of asci. (× 500; *after Guillermond*, 1909.)

nucleus of the hyphal cell divides; one daughter nucleus remains behind in the hyphal cell, the other wanders out into the copulation branch. and fuses there with the nucleus of the other branch (Fig. 85, 4 to 8), The zygote (the bend of the copulation bridge) swells up to an ascus, which is abjointed from the copulation branches; its nucleus divides thrice and the eight spores are surrounded by a double membrane (Fig. 85, 9 and 10); occasionally some spores remain behind in development and degenerate.

The spores are liberated by disintegration of the asci. At germination the spores swell to twice the size, rupture the exospore to form one or more germ tubes which, after repeated nuclear division, develop to hyphae.

In addition to this normal development, cases of parthenogenesis occur occasionally; two copulation branches may swell to asci without copulation; similarly, a copulation branch which finds no partner may develop independently (Fig. 85, 11); besides, especially in old cultures,

even the hyphal cells, though they earlier may have formed a copulation branch, swell up themselves parthenogenetically to asci (Fig. 85, 12 to 14), which are generally smaller than the diploid, but like the latter, may have eight spores or some spores may abort.

From the type of *Eremascus fertilis*, there are two developmental series, one includes isogamous forms like *E. fertilis*, the other heterogamous forms. Both, however, may develop parthenogenetically.

In the isogamous series there may be directly connected to *E. fertilis*, the *Endomyces fibuliger*, originally isolated from spoiled bread. Its hyphae are always uninucleate, and show (in contrast to *Eremascus fertilis* a tendency to disintegrate into oidia which develop to a sprout mycelium. Furthermore, the hyphal cells also may proceed to sprouting (Fig. 87, 8).

This development from sprout mycelium is apparently connected with an extensive adaptation of the fungus to starch and sugar-containing media: thus *Endomyces fibuliger*, in contrast to *Eremascus fertilis*, is able to ferment sucrose and some monosaccharides. Wherever the

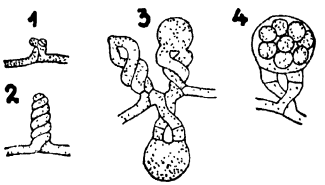


FIG. 86.—*Eremascus albus*. Development of copulation branches and ascus. (× 600; *after Eidam*, 1883.)

budding cells arise on aerial mycelium, the diameter is smaller and the wall somewhat thicker than in the submersed sprout cells. They are then very resistant and survive a long period in temperatures up to 55° C. Biologically, they apparently possess the significance of gemmae and, because of the exogenous formation, may be designated as conidia.

As in *Eremascus fertilis*, any two cells form copulation branches which may approach each other; only very rarely however, after the dissolution of the wall, are the two nuclei joined into a fusion nucleus (Fig. 87, 1). Generally the copulation branches develop parthenogenetically, even when the separating walls are temporarily dissolved (Fig. 87, 5). As an exception, a pseudogamous anastomosis of two sprout cells may occur in which one changes to an ascus (Fig. 87, 2 to 4).

In a large number of cases, no copulation branches are formed but the asci, like the sprout cells, arise as lateral outgrowths of the hyphal cells (Fig. 87, 6 and 7); then, however, they are three to four times larger than the ordinary sprout cells. Occasionally they arise from ordinary hyphal cells by swelling, or from swelling sprout cells. When they begin to appear the formation of sprout cells slows up, but does not

cease, and thus hyphae may form sprout cells and asci simultaneously. One finds even young asci which continue to cut off sprout cells until they begin spore formation. Periods of vegetative growth and fructification are thus not sharply separated from each other.

The asci contain four spores of a peculiar hat shape, such as we shall meet later in *Endomyces decipiens* and in *Willia* of the Saccharomycetaceæ. At germination they throw off the exospore and germinate with either germ tube or sprout mycelium (Dombrowski, 1902; Guillermond, 1909, 1910*b*, 1913*a*).

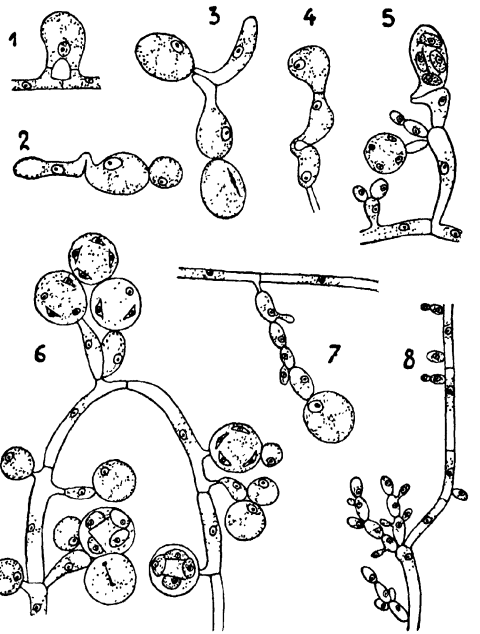


FIG. 87.—*Endomyces fibuliger*. Development of asci. (× 500; *after Guillermond*, 1909.)

In contrast to *Eremascus fertilis*, in *Endomyces fibuliger* sexuality is so completely weakened that the sexual organs may only be explained as vestiges. In a large number of cases, no copulation tubes are formed and the asci arise directly from vegetative hyphae or sprout cells.

In the following forms, the copulation branches no longer fuse, they are formed less frequently and the asci arise parthenogenetically throughout. The growth of mycelium through sprouting increases proportionally. In two Chinese species, *E. Lindneri* and *E. Hordei*, the copulation branches no longer change directly to asci but develop to a short, occasionally branched mycelium (Fig. 88, 1 and 2), on which the asci arise by swelling of the hyphal cells. In the majority of cases the asci

e formed directly from the sprout cells, without this detour (Mangenot, 22). Both species ferment sucrose and a series of monosaccharides.

In two other species which terminate the isogamous development, *ndomyces javanensis* and *E. capsularis* (*Saccharomycopsis capsularis*), e copulation branches have entirely disappeared (Fig. 88, 3 to 5). ccording to cultural conditions, either the hyphal or sprouting condition eponderates. At the end of the hyphae, there arise by swelling of cells by lateral sprouting, at times also intercalary, four-spored asci whose ores are divided into two unequal halves by annular thickenings uillermond, 1909). Both species have been isolated from earth, e former in Java, the latter in the Swiss Alps. In both, the fermentave ability is small.

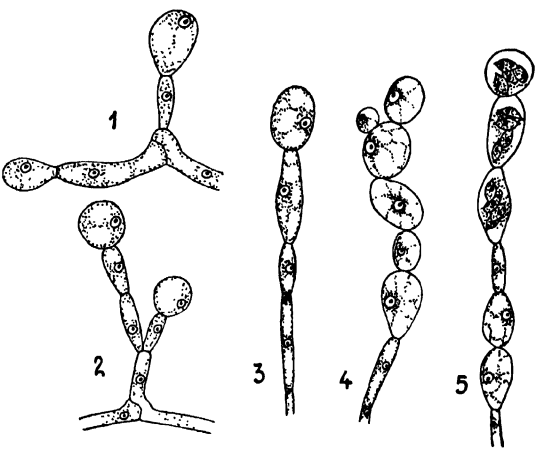


FIG. 88.—*Endomyces Lindneri*. 1, 2. *E. capsularis* 3 to 5. Development of asci. (1, × 470; 3 to 5 × 500; *after Mangenot*, 1922, and *Guillermond*, 1909.)

The second, heterogamous series is connected to the *Eremascus fertilis* pe through *Endomyces Magnusii*, found in the slime-flux of trees. Its phae are generally multinucleate (2 to 8); in the growing hyphal tips e number of nuclei may mount to 50 (Fig. 89, 1), in weak hyphae it ay sink to one. In contrast to *Eremascus fertilis*, and like *Endomyces uliger*, the hyphae divide easily into oidia; naturally these are generally ultinucleate, rarely uninucleate, with a tendency toward the uninueate condition. Often they thicken the wall and become gemmae ig. 89, 14); hence under certain conditions, *e.g.*, in Raulin's solution, e whole culture may disintegrate after two weeks into oidia which ange into gemmae.

Under favorable conditions the oidia, as in *E. fibuliger*, may develop sprout mycelia. This, however, does not take place by the indendent development of the small outgrowths of the mother cell to sprout

cells, but by the fission of the mother cell so that both daughter cells round off and develop to the size of the mother cell (cell division, in contrast to sprouting).

When the mycelium is ready to form asci, it assumes a characteristic habit: it branches into numerous, short, slender branches with short cells which contain only a small number of nuclei, often only one (Fig. 89, 3 and 4). The branches end either in a very large cell full of reserves, the female copulation branch, or in a narrow, often twisted branch with hyaline content, the male copulation branch. The upper third of the female copulation branch swells considerably and collects the cytoplasm

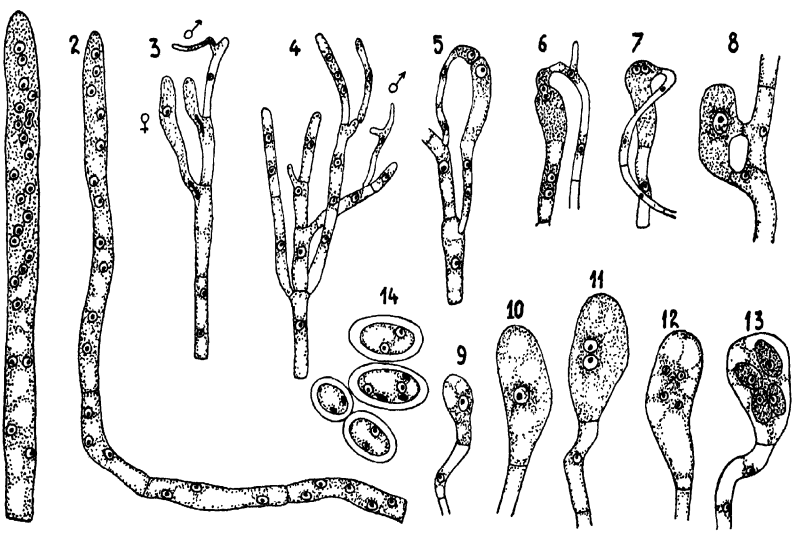


FIG. 89.—*Endomyces Magnusii.* 1. Young multinucleate hypha. 2. Older hypha. 3 to 13. Development of asci. 14. Gemmae. (1, 2, 14 × 1,500; 3 to 13 × 500; *after Guillermond*, 1909.)

with two or three nuclei. At the beginning of copulation, it bends over somewhat to meet the male copulation branch. In this stage, the swollen part contains only one nucleus, the others have migrated downward (Fig. 89, 5). The narrow male copulation branches contain one to three nuclei when young, of which only one remains at the tip.

In approximately three-fourths of the cases, copulation occurs between the male and the female copulation branches. The male copulation branch approaches the female, swells slightly and abjoints the apical uninucleate gametangium from the stipe cell. Meânwhile the uninucleate tip of the female copulation branch is abjointed from the stipe cell. Hereupon the walls separating the gametangia are dissolved and the zygote develops to a 4-spored ascus (Fig. 89, 6 to 8).

In addition to this usual course of development, there occur also numerous variants; thus, the male copulation branch may approach the female at the side instead of the tip (Fig. 89, 8); or the copulation branches may contain only a single nucleus with no abjunction of the stipe cell; or the female gametangium may develop parthenogenetically without copulation (Guillermond, 1909).

In *Endomyces decipiens*, which is also characterized by the type of cell multiplication but contains uninucleate cells, sexual organs are almost entirely absent (Brefeld, 1891; Dangeard, 1907; Juel, 1921). It is parasitic on fructifications of *Armillaria mellea* and fruits in the lamellae. The asci arise on the hyphae as small branches which swell into sacs and

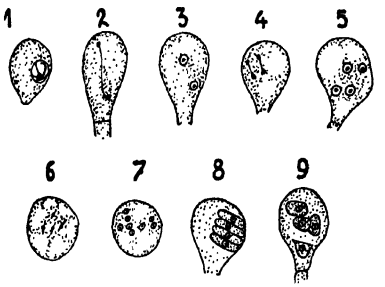


FIG. 90.—*Endomyces decipiens*. Development of asci. (× 800; *after Juel*, 1921.)

are abjointed from the hypha. As a rare exception, a sexual act takes place (isogamously!). Although occasionally three nuclear divisions occur in the asci, they always contain only four spores which, as in *E. fibuliger*, are cucullate. In cultures, the hyphae break up into uninucleate oidia. On branches they form thick-walled, yellowish gemmae the size of asci which, under suitable conditions, germinate with one or more germ tubes. *E. decipiens* has reached the same height as *E. javanensis* and *E. capsularis* in the isogamous series.

Let us review the course of presentation. The Endomycetaceae contain some forms with completely developed sexuality, such as *Eremascus fertilis* and the heterogamous *Endomyces Magnusii*. Their life cycle may be illustrated as follows:

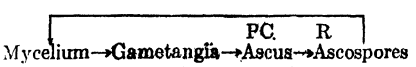


DIAGRAM XIV.

Thus the gametangia which copulate without further differentiation arise on a hermaphrodite mycelium. The zygote develops to an ascus in which 4 to 8 ascospores are formed by meiosis. This life cycle is essentially the same as *Dipodascus*, *Basidiobolus*, *Entomophthora*, etc.

In *Eremascus fertilis*, the division of the hyphal nucleus before copulation is strongly reminiscent of *Basidiobolus*, in *Endomyces Magnusii* the extrusion of the supernumerary nuclei is reminiscent of *Endogone*. Only the zygote in *Basidiobolus* and *Endogone* develops to a hypnospore, while in *Eremascus fertilis* and *Endomyces Magnusii* to a sporangium in which are formed the ascospores which function as hypnospores.

From these sexually well-developed forms, there may be observed a gradual decline of sexuality. Thus in a second stage, *Endomyces fibuliger*, the copulation branches can still copulate; however, they usually develop parthenogenetically, so that the life cycle almost disappears in the haploid phase:

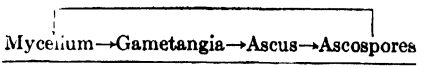


DIAGRAM XV.

Nevertheless, in *E. fibuliger* sexuality is not entirely suppressed; it is possible for two sprout cells to copulate; no special sexual organs are used, but the sexual act is shifted into the thallus and takes place pseudogamously:

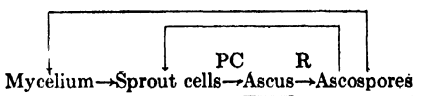


DIAGRAM XVI.

Finally, in the third and last stage, *E. javanensis* and *E. capsularis*, the functionless gametangia are no longer formed; similarly, the sexual act no longer takes place between two vegetative cells, and the thallus mostly disappears in a sprout mycelium. Thus the life cycle is as follows:

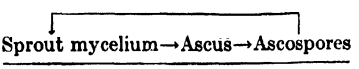


DIAGRAM XVII.

Herewith morphologically we arrive at the stage of the yeasts. Before we proceed to the discussion of this family, two more genera, *Pericystis* and *Ascoidea*, should be briefly mentioned, which, although insufficiently known, certainly belong in the vicinity of the Endomycetaceae. *Pericystis apis*, the cause of chalk brood of bees, is a heterothallic form in which the sexual dimorphism marks even the habit of the mycelium. A multispored ascus is formed by copulation of two gametangia of unequal size (Claussen, 1921). *P. alvei* (A.D. Betts, 1912) occurs on stored pollen in beehives.

Ascoidea rubescens forms a thick reddish-brown mass in the slime-flux of beech. It is composed of felt-like tissue of ramose, septate hyphae,

whose membrane is hyaline in youth, but appears brownish in age. Hyphal ends swell to conidia. Lateral outgrowths of hyphae form new conidia which push aside the previous ones so that finally a tuft of as many as 30 conidia is formed (Fig. 91, 1). The conidia are quite variable in size; in general the earlier ones are larger than the later. They germinate with germ tubes which, with liberal nourishment, grow into mycelia or, with poor nourishment, form new conidia (Fig. 91, 2).

After a time, the conidia are gradually replaced by asci (?). The hyphal ends swell as in conidial formation, abjoint, and change into

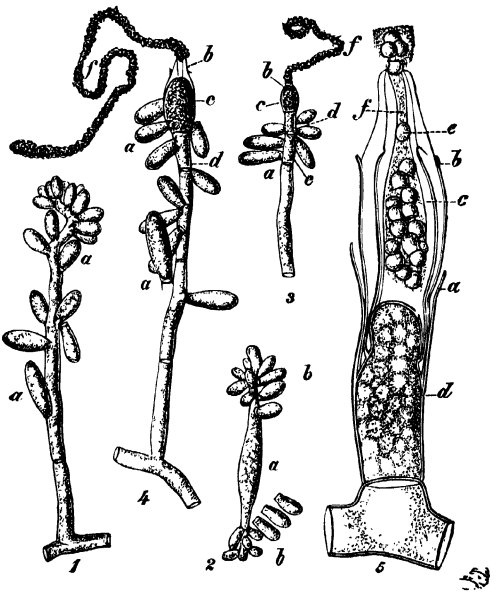


FIG. 91.—*Ascoidea rubescens*. 1. Conidiophore and conidia, *a*. 2. Conidium, *a*, germinating under unfavorable conditions, cutting off conidium, *b*. 3, 4. Conidial and ascigerous hyphae, *a*, conidia; *b*, ascus discharging spore mass, *f*, while the second ascus, *c*, forms within the wall of the first; *d*, *e*, ascus fundaments. 5. Ascigerous hyphal tip; *ac*, evacuated ascus walls; *d*, youngest ascus fundament, *e*, spore in the gelatinous sheath, *f*. (1, 3, 4 × 80; 2 × 120; 5 × 540; *after Brefeld*, 1891, *and Tavel*, 1892.)

multinucleate asci. After many nuclear divisions, its contents divide into numerous small, uninucleate, cucullate spores which at first are joined in pairs. Corresponding to the variable size of the ascus, they are also indefinite in number; however, they are distinguished by a remarkably regular form, similar to that of *Endomyces decipiens*. Like the *Mucor* spores, they are embedded in a finely granular, strongly swelling intermediate substance. At maturity this expands greatly with water absorption, pushing from the strongly swelling sporangial tip like a screw, and, together with the imbedded spores, is liberated as a vermiform mass

(Fig. 91, 3 to 5). After repeated nuclear division, the spores germinate within the intermediate substance by germ tubes which usually proceed again to conidial formation. The complete evacuation of the ascus is only effected by the stipe cell beneath developing to a new ascus; in proportion as this new structure bulges upward, the remainder of the spore mass is pushed out. This sporangial proliferation may be repeated up to twelve times; it is very reminiscent of the relationships of the Saprolegniaceae where it is placed by Lohwag (1926). Unfortunately, the cytological details of the life cycle of this interesting species are still insufficiently known; possibly it develops parthenogenetically (Brefeld, 1891; Popta, 1899; Lohwag, 1926).

Saccharomycetaceae.—The yeasts may be regarded as direct derivative of the Endomycetaceae in which the growth of the thallus by sprouting has become entirely prevalent. Some forms, as *Saccharomycodes Ludwigii*, *Debaryomyces Kloeckeri*, *Zygosaccharomyces Priorianus* and *Pichia membranifaciens*, under certain conditions of nourishment, *e.g.*, on gelatin substrates, can still form true hyphae; these are unstable, however, and with a slight alteration of the substrate break up into sprout mycelia.

The sprout cells are generally spherical or ellipsoidal, and hyaline, the size varying according to substrate and age. Under unfavorable conditions they can store fat and glycogen and surround themselves with a double membrane. These resting cells are very resistent to environment and can carry over unfavorable periods; probably they correspond to the gemmae in *Endomyces*. At germination, the outer fragile wall is ruptured and the cells grow into a sprout mycelium.

We may distinguish two tribes of the Saccharomycetaceae according to the type of cell multiplication. In the Schizosaccharomyceteae, it takes place as in *Endomyces Magnusii:* the cells elongate; when they have attained a certain size they divide by septa into two daughter cells each, which round off, separate, grow and divide similarly. These types are chiefly of southern origin and at present only a few are known. In the other group, the Saccharomyceteae, the sprout cells are formed, as in *Endomyces fibuliger*, as small lateral protrusions of the mother cell; they are abjointed, increase in size and finally attain the appearance of the mother cell. This second tribe includes the greater part of the known yeasts technically used as ferments. These two tribes are not as sharply separated as would seem at first sight, thus *Saccharomycodes Ludwigii* generally follows the first tribe but it may also increase by sprouting. The sprouts are only formed at the poles, not at any spot as is usually the case in yeasts.

If the sprouting proceeds rapidly, the daughter cells may sprout further (and in *Schizosaccharomyces* divide) before they are separated from the mother cells. Thus there are formed small colonies and, in old cul-

tures, long filaments. As far as is known, in all these cell multiplications nuclear divisions are amitotic (Fig. 95, 1 to 4).

Under certain conditions of nourishment, especially in age, with the exhaustion of nutrient, or on solid substrates like gypsum blocks, asci with ascospores appear in the cultures, as in the Endomycetaceae. This character distinguishes the family from numerous other families discussed in this book, belonging to other groups which also may form a sprout mycelium, and especially also from the imperfect yeasts, as *Torula*, *Mycoderma*, "*Dematium*," *Cryptococcus* and *Monilia*.

In the wild yeasts, the number of ascospores varies from one to twelve; in many industrial yeasts, certain numbers predominate, thus in *Schizosaccharomyces octosporus* 4 or 8, in *Saccharomyces cerevisiae* and the yeast Johannisberg II 4 and in *Saccharomyces Pastorianus* 2. They are very resistant and, in the wine yeasts, may winter over in the soil of the vineyard. Generally they are spherical or oval; in *Willia anomala*, as in *Ascoidea* and *Endomyces fibuliger*, they are hemispherical, with the flat wall projecting over the edge like a hat brim. In *Willia Saturnus* they are citriform and (like *Endomyces capsularis*) provided with an equatorial projecting ring; in *Pichia membranifaciens*, they are irregular, spherical, hemispherical to tetrahedral; in *Nematospora*, they are fusiform and provided with a slender appendage at each end. They are generally smooth, but rough in *Debaryomyces* and *Nadsonia*. In contrast to the majority of the Endomycetaceae, the wall is usually one layered; in *Saccharomycopsis guttulatus*, two layered, as in the Endomycetaceae, in which case the outer layer ruptures on germination.

The processes in the formation of ascospores may be next discussed in connection with *Schizosaccharomyces octosporus*, on figs and grapes in the Mediterranean region (Guillermond, 1903, 1905, 1910, 1917; Coker and Wilson, 1911). About three days after the culture is made the cells copulate in pairs by short tubes (Fig. 92, 1 to 6). In cell chains, it occasionally happens that the separating wall between two sister cells is dissolved (adelphogamy). Two nuclei migrate into the copulation canal and fuse; the copulation canal broadens and the two individuals develop into a barrel-shaped structure in which, within approximately a half-hour, after three or more, rarely two, nuclear divisions, eight—rarely four—spores appear (Fig. 92, 7 to 22). Often the copulation canal does not attain the breadth of the mother cell, and the young ascus is shaped like a dumbbell between whose ends the eight spores are divided. At germination the spores in the ascus swell, the ascus wall ruptures, the spores are freed, and each is divided by a septum into two daughter cells which later divide in a similar manner.

Under unfavorable conditions, copulation may occur earlier, so that already in the ascus the ascospores copulate with spores of the same or neighboring ascus. Other cultures have a tendency to become aspor-

ogenous; these may still form processes; since many cells no longer take part in copulation, however, these are forced to grow long distances; or they grow past each other and no longer copulate. Exceptionally in some cells, four spores may arise parthenogenetically, the other cells may develop purely vegetatively.

This life cycle of *Schizomaccharomyces octosporus* may be connected directly to that of *Endomyces fibuliger*. In this species, two sprout cells may copulate with each other; only in *E. fibuliger* one sprout cell becomes an ascus, while in *S. octosporus* the sexual act is isogamous. Gametangial copulation, which in *Eremascus fertilis* was the only form of sexuality and in *Endomyces fibuliger* was partially replaced by pseudogamy (copulation of two vegetative cells), in *S. octosporus* is entirely suppressed

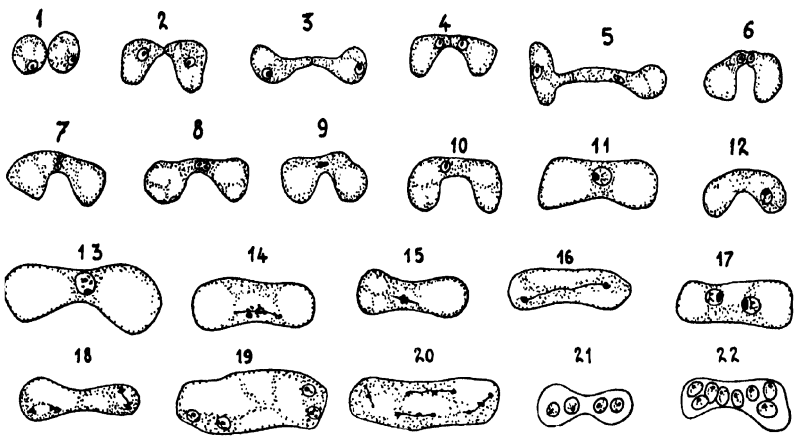


FIG. 92.—*Schizosaccharomyces octosporus*. Copulation and development of asci. (× 750; *after Guillermond*, 1903, 1905, 1917.)

and replaced by pseudogamy. This also disappears, and the cells, after unfruitful attempts at copulation, may change parthenogenetically to asci or, without this attempted copulation, may develop asci directly and vegetatively.

In the other Schizosaccharomyceteae, sexuality and spore formation degenerate still further. Thus in *S. Pombe*, the yeast of a negro beer, and in *S. Mellacei*, a yeast occurring in the rum factories of Jamaica, numerous asporogenous strains are known and in *S. asporus*, the yeast of arak manufacture in Java, no spores are known.

While in the Schizosaccharomyceteae, the fertilization has become chiefly isogamous, in the Saccharomyceteae there appears a tendency to heterogamy and pedogamy. The simpler forms, as *Zygosaccharomyces Barkeri* (Barker, 1901), *Z. Priorianus* and *Willia anomala* (Guillermond, 1911*a*), like *Schizosaccharomyces octosporus*, may be connected

directly with the pseudogamous development of *Endomyces fibuliger* (Fig. 87, 2 to 4). Two cells form a copulation process toward each other (Fig. 93, 1 to 5) the nuclei migrate into the bridge and fuse, the diploid nucleus divides, both daughter nuclei migrate back into copulation cells, there divide a second time, and in each fusion cell two spores arise. The dumbbell structure corresponds to an ascus. In some cases, at least in *Z. Priorianus*, copulation is absent and the individual sprout cells develop parthenogenetically to asci. Exceptionally, especially in small colonies, if the cultures are transplanted into conditions of nourishment which stimulate them to copulation and spore formation,

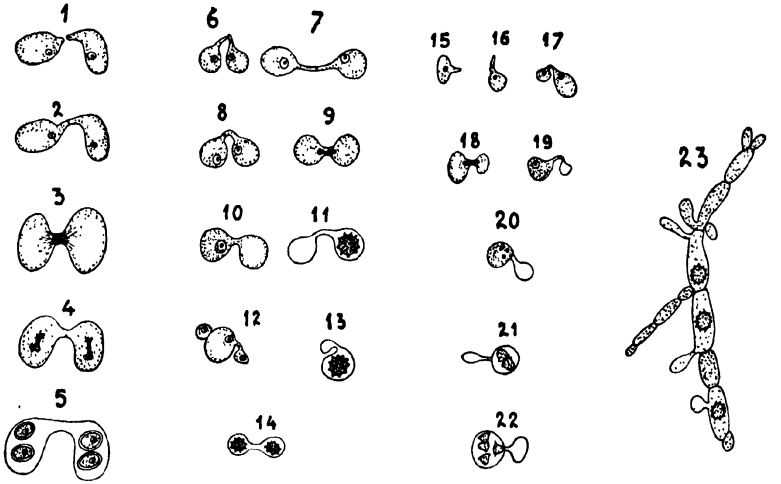


FIG. 93.—*Zygosaccharomyces Barkeri.* 1 to 5 (× 650). *Debaryomyces globosus.* 6 to 14 (× 1,000). *Zygosaccharomyces Chevalieri.* 15 to 22. (× 670). *Debaryomyces Kloeckeri.* 23 (× 1,000). Copulation and development of asci. (*After Barker,* 1901; *Guillermond,* 1912; *Guillermond and Péju,* 1920.)

the mother cell, for lack of other cells, will copulate with a daughter cell. Thus, exceptionally, the sexual act may be pedogamous.

That which was an anomaly in *Zygosaccharomyces Priorianus,* however, becomes increasingly common in the following forms; simultaneously, copulation, because of the weakening of the sexual tendencies, becomes more and more difficult. Thus, in *Debaryomyces globosus* from the Antilles, approximately 75 per cent of the asci are parthenogenetic. Occasionally copulation branches are still formed, which for lack of sexual attraction, grow by each other. In about 25 per cent of the cases, a sexual act occurs. This may take place between two mature individuals in which the diploid nucleus either divides in the bridge and returns a daughter nucleus to each fusion cell or withdraws undivided

into a fusion cell and there forms a spore (Fig. 93, 6 to 11); it may just as often occur, however, between a still sprouting mother cell and a young daughter cell (Fig. 93, 12 to 14) where the content of a daughter cell migrates back into a mother cell (Guillermond, 1912*a*).

This pedogamous form of the copulation becomes the normal in the following species. The West African *Zygosaccharomyces Chevalieri* and the west European *Z. Pastori* and *Z. Nadsonii*, in the Russian *Debaryomyces tyrocola*, in the French *D. Kloeckeri* and in the Russian *Nadsonia fulvescens* and *N. elongata* (Nadson and Konokotina, 1911, Konokotina, 1913; Guillermond, 1918, 1919, 1920; Guillermond and Peju, 1919, 1920 and 1921). Exceptionally there is no difference between the fusion cells, and the daughter cells have already developed to the size of the mother cell (Fig. 93, 15 and 16). In most cases, copulation takes place (in case it is still necessary and is successful) between a mother cell and a daughter cell which has just been formed (Fig. 93, 17 to 23); generally the content of smaller cells returns to that of the larger, which is abjointed and develops to a 1 to 4 spored ascus, while the smaller fusion cell disappears. Besides, especially in *Zygosaccharomyces Chevalieri*, with insufficient nourishment the two ascospores may copulate after they have swollen and ruptured the ascus wall or an ascospore may copulate with a sprout cell and change into a one-spored ascus, or the ascospore, without any copulation, may function as an ascus and form ascospores within.

In *Nadsonia* (*Guilliermondia*), spore formation does not generally occur inside the larger fusion cell; on the side opposite the copulation canal, a sprout cell receives the united contents of both fusion cells and changes into 1 to 2 brown-walled spores. It is still obscure whether this relationship has a deeper significance and whether one may ascribe to it in principle the same significance as to the development of the ascogenous hypha of the typical Ascomycetes.

From this paedogamous group, the lines diverge to entire parthenogenesis and to diploid sprout mycelium.

The starting point of the first series is *Zygosaccharomyces Pastorii* and its relatives. In this group, as earlier in *Debaryomyces globosus*, although many cells form copulation processes, only a few are able to copulate because of increasing weakening of sexuality. This character continues in *Torulaspora Delbrueckii*, in English beer, and in *T. Rosei*, in slime flux of oak. On favorable media the sprout cells form numerous copulation tubes and seem to attempt to anastomose with each other. (Fig. 94, 1 to 3). Often they lie so close that the pressure of the cover glass no longer suffices to isolate them. Exceptionally, the cell content migrates to the copulation bridge and there, after a sexual act, the ascospores arise. Generally the separating wall is no longer dissolved, but each cell forms 1 to 4 spores parthenogenetically (Guillermond, 1912*a*).

In *Schwanniomyces occidentalis*, on earth in the Virgin Islands, dynamic sexuality is lost and morphologically only a few traces remain. At sporulation the cells which will develop to asci form longer or shorter copulation processes. Their sexual attraction is so small that they are only seldom

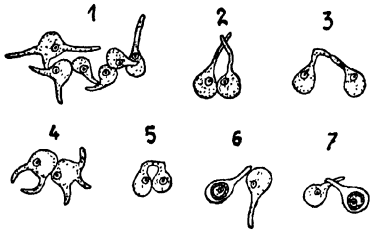


FIG. 94.—*Torulaspora Rosei*. Development of asci. (× 1,000; *after Guillermond*, 1912.)

able to join and, even when this happens, they no longer come into open communication but change parthenogenetically to asci.

From this species, it is only a short step to purely parthenogenetic forms in which no traces of sexuality are retained either dynamically or morphologically and in which the ascospores under suitable conditions

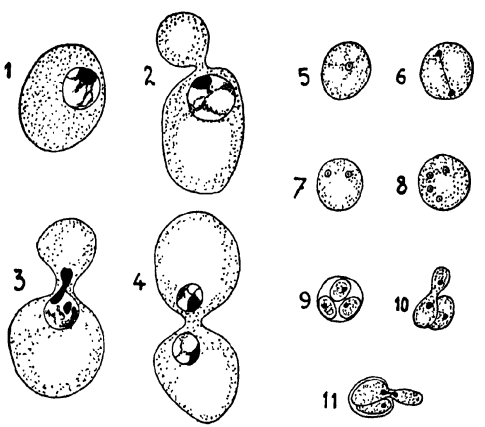


FIG. 95.—*Saccharomyces cerevisiae*. 1 to 4. Formation of sprout cell with amitosis of nucleus. (× 1,500.) 5 to 11. Development of sprout cell to ascus and germination of ascospore. (× 750.) (*After Guillermond*, 1902, 1904.)

are formed directly as endospores in any vegetative cells (Fig. 95, 5 to 9). This parthenogenetic group contains many technically important species discussed in detail in Lafar, *Handbuch der technischen Mykologie*, as *Saccharomyces cerevisiae*, the group of beer yeasts; *S. Pastorianus*, cause of a beer disease; *S. ellipsoideus*, the collective type of the more important wine yeasts; *S. minor*, a yeast of bread making; and *Pichia membranifa-*

ciens, a wild yeast. With the disappearance of sexuality in many of these forms, spore formation also disappears, and in them there are known numerous asporogenous strains, hereditarily fixed.

The starting point of the second series, which leads to the diploid character of sprout mycelium, is formed by *Zygosaccharomyces* and its relatives. In this form, as in *Schizosaccharomyces octosporus*, the ascospores, immediately after their liberation from the ascus, may copulate with one another or with vegetative cells or they may change parthenogenetically to new asci. This has been observed only as an exception in *Zygosaccharomyces Chevalieri*, but is the rule in the following groups: the west African *Saccharomyces Chevalieri*, *S. Mangini*, *S. ellipsoideus*, in *Willia Saturnus*, on earth in the Himalayas and in *Nematospora* (Guillermond, 1910, 1914). At germination the spores swell and rupture the

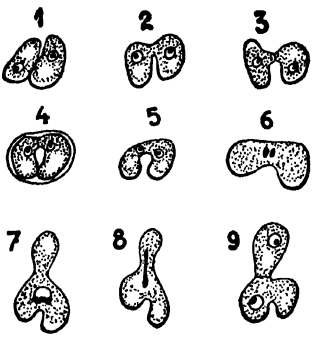


FIG. 96.—*Saccharomyces ellipsoideus*. Copulation and development of asci. (× 750; *after Guillermond*, 1905.)

ascus wall. Some of them grow normally to a sprout mycelium. Some, before, during or after the rupture of the ascus wall, copulate in pairs (Fig. 96, 1 to 6). In contrast to *Zygosaccharomyces Chevalieri*, the zygote does not change into an ascus but sprout cells, which develop to an apparently diploid sprout mycelium, appear in the copulation canals, occasionally also on the whole upper surface of the copulating cells (Fig. 96, 7 to 9). Later, without further sexual processes, as in *S. cerevisiae*, the ascospores arise in the vegetative cells.

The end of this second series is formed by *Saccharomycodes Ludwigii* in slime flux of oak (Guillermond, 1903, 1905). Its asci almost always contain four spores which lie in pairs at the two poles (Fig. 97, 1 and 2). The spores at one pole result from the division of one nucleus; thus they are sister cells and remain connected by a protoplasmic layer remaining from the periplasm. At germination they swell much in the ascus and form small beaks toward each other which broaden to copulation canals (Fig. 97, 1 to 4). At times several spores fuse. Two cells of the same

tendency often attract a third of different tendency. Occasionally copulation may be retarded and the tubes attain a considerable length or, as the ascus is torn by them, they may grow into the open. Furthermore, the copulation processes may go in a meridianal direction and fuse with the spores of the other pole; or the spores may develop unsimultaneously or abort, in which case fusion with spores of another ascus may occur (Fig. 97, 9). Finally, as an exception, the spores may germinate parthenogenetically, especially in old cultures, in which case there results a special strain which only germinates parthenogenetically; it does not differ morphologically from the original strain, and forms a germ tube which ruptures the ascus wall.

After the copulation processes have come into open communication, the nuclei migrate into the bridge and fuse (Fig. 97, 6 and 7); occasionally the fusion may occur in one of the spores instead of in the canal or may

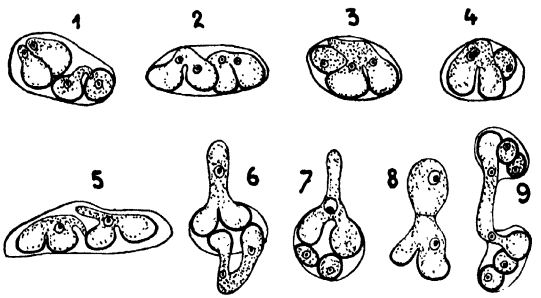


FIG. 97.—*Saccharomyces Ludwigii.* Copulation and development of asci. (× 750; *after Guillermond*, 1905.)

be retarded and take place only in the germ tube which grows out of the copulation canal, breaks through the ascus wall and germinates to a sprout mycelium.

If one imagines this copulation entirely suppressed (as occurs in certain strains), one arrives, as in the *Torulaspora–Schwanniomyces* series, to asexual forms of *Saccharomyces cerevisiae.* Only these forms, in contrast to the former, would be regarded as apogamous since their thallus belongs to the diplonts. The forms of the *S. cerevisiae* type thus may be considered biphyletic, where it is not easy to distinguish which belong to the parthenogenetic and which to the apogamous groups. It need hardly be said that in reality the roots of these asexual forms are much more numerous and that the Saccharomycetaceae form a polyphyletic family since *Endomyces capsularis* and its relatives could have led directly to such forms.

In order to demonstrate more clearly the present conception formulated by Guillermond, the different forms have been connected according to the similarity which they show in the point of view given in our treatment on page 156.

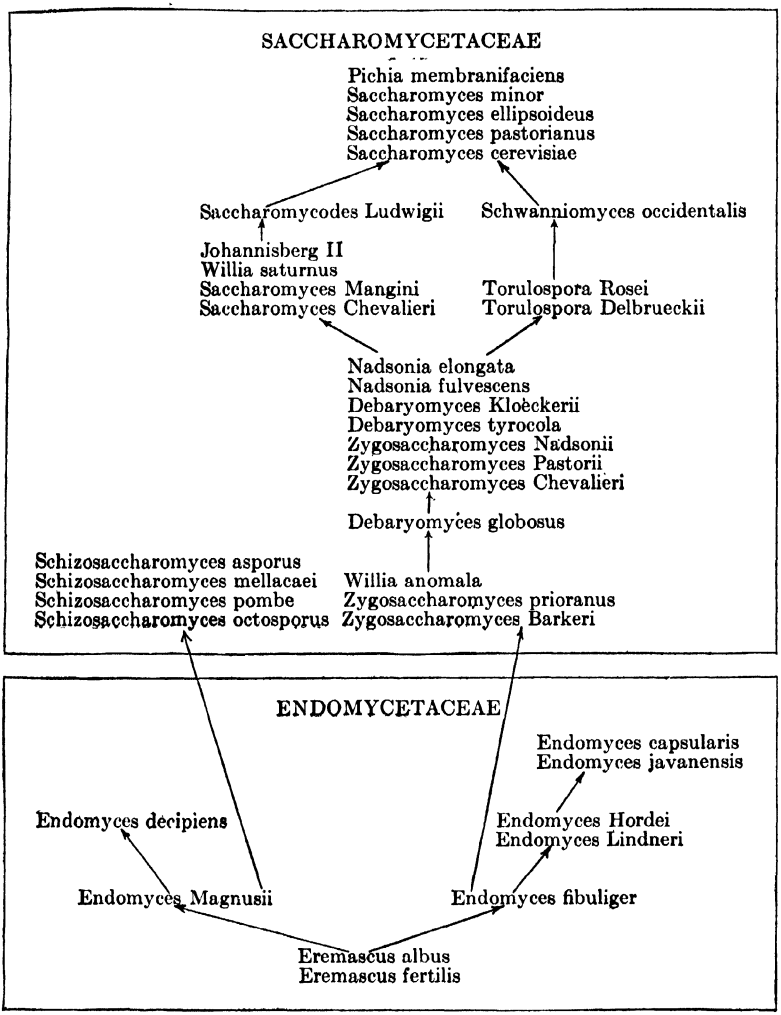


DIAGRAM XVIII.

The isogamous *Eremascus* forms the beginning from which two branches separate, an isogamous (with sprout cells) and a heterogamous (with cell division); both end with chiefly parthenogenetic forms (*Endomyces decipiens* and *E. capsularis*). As the Saccharomycetaceae still possess true sexuality they cannot result from these end forms but they must branch off earlier, *e.g.*, at the level of *E. Magnusii* and *E. fibuliger*.

The family of the Saccharomycetaceae is divided into two lines, according to whether the development of their sprout cells agrees with

one or the other of the Endomycetaceae lines: the Schizosaccharomyceteae are connected with *Endomyces Magnusii* and the *Saccharomyceteae* with *E. fibuliger*. The justification of this separation is uncertain, as there are transitional forms between the two lines, *e.g.*, *Saccharomycodes Ludwigii*.

In both lines a reduction of the thallus has arisen as a result of their mode of life: in general, they form only sprout mycelium. This degeneration of the thallus is followed by a degeneration of the sexual organs; whereas the thallus is habitually altered until unrecognizable, they have been able to retain traces of the form of the sexual act; gametangial copulation of *Eremascus* has been lost but the pseudogamous substitute, which has already appeared in *Endomyces fibuliger*, is retained unaltered in the primitive Saccharomycetaceae.

Both in the Schizosaccharomyceteae and the Saccharomyceteae, the pseudogamous sexual act still is isogamous. While the former rapidly develop apospory, the latter undergo a peculiar development toward heterogamy. They are heterogamous as regards their products while the sexual act is still isogamous (no longer the copulation canal, but one of the copulation cells becomes the ascus); then they become heterogamous as regards the sexual act (larger and older or better nourished cells copulate with smaller, younger or poorer cells). From this dynamic heterogamy, pedogamy and adelphogamy result. Thus paedogamy, at least in the Saccharomycetaceae, may be considered a sign of retrogression.

Hand in hand with these morphological and dynamic changes, goes a weakening of the sexual act. The forms develop increasingly asexually and the sexual act is completed in a smaller per cent of individuals. Also the sexual act becomes more labile in this relation. It can occur earlier and take place between two spores in an ascus. But it appears to be completed with difficulty because of a lessening sexual power; copulation tubes may still be formed, but they grow by, for they are no longer attracted to, each other. Finally, the sexual act may be wholly suppressed and the forms develop apomictically, which brings us to the same stage reached in the Endomycetaceae by *Endomyces decipiens* and *E. capsularis*.

In the scheme on page 156, sexual act and sexuality have changed in form, place, time and content between the stages of *Eremascus fertilis* and *Saccharomyces cerevisiae*. In form, it develops from gametangial copulation to pseudogamy which becomes paedogamy, either of a parthenogenetic or an apogamous type. In place, the sexual act occurs normally in the thallus, then in the gonotoconts, the asci. At first it normally closes the vegetative period, while later it begins it. In content, the sexual act is first a copulation of the principal fruit form, the asci, later this beeomes unnecessary and disappears.

If this concept is correct, then *Saccharomycodes Ludwigii* cannot be, as some authors (*e.g.*, Nadson, 1911) have assumed, a primitive form, but

must be considered a degeneration stage in our scheme of relationships, like its analogue in the Ustilaginales. This is much simpler as diplontic Endomycetaceae, which might be considered ancestors of *S. Ludwigii*, are unknown.

Atichiaceae.—Before we leave the yeasts, we should mention a group which has long puzzled mycologists. It has been placed in the Floridieae, Fucaceae, Lichenes, Saccharomycetaceae, Perisporiaceae, Capnodiaceae, Myriangiaceae, Ascocorticiaceae and Bulgariaceae. *Atichia* forms

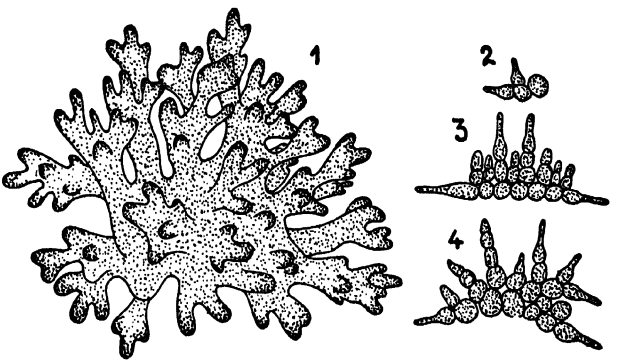


FIG. 98.—*Atichia glomerulosa*. 1. Thallus. 2 to 4. Propagula. (1 × 80; 2 to 4 × 400; *after Neger*, 1918.)

gelatinous cushions on leaves and needles, apparently as epiphytes (Fig. 98, 1). These cushions are formed of sprout cells which develop ascospores in the superficial layers. Under favorable conditions these cells develop into a multitude of three-rayed reproductive bodies, called **propagula** (Fig. 98, 2 to 4), which are disseminated by wind and rain. They develop again to cushions (Hoehnel, 1910; Cotton, 1914; Neger, 1918). Perhaps they are highly developed yeasts, adapted to an epiphytic existence, but one may not entirely discard the concept of a degeneration of simple Discomycetes.

CHAPTER XII

TAPHRINALES

In the Taphrinales, some hyphal cells may swell to more or less thick-walled chlamydospores (gemmae) which immediately after formation or after a winter's rest, germinate to an ascus. Ascospores do not arise, as in the typical Ascomycetes, in the free space of the ascus, but are cut out of a protoplasmic layer, adjacent to the wall.

At present only parasitic forms of the Taphrinales are known. According to the number and method of formation of the ascospores, they fall into two families, the Protomycetaceae and the Taphrinaceae. In the Protomycetaceae, each of the spore mother cells, present in an indefinite number along the walls, divides into four ascospores, endospores. In the Taphrinaceae, they arise in fours or eights by free cell formation, as in the typical ascus, from the protoplasmic layer at the wall.

Protomycetaceae.—The life cycle of this family will be discussed for two of the best known representatives, *Protomyces pachydermus* and *P. macrosporus;* the former is found on *Taraxacum officinale;* the latter, in various biological strains, is more or less sharply specialized on various Umbelliferae; both cause callosities on the stems and leaves of the host (Popta, 1899; Büren, 1915, 1922).

Their hyphae are intercellular, the cells are multinucleate. They swell to intercalary or terminal chlamydospores (Fig. 99, 15). From youth these are multinucleate and the nuclei are often paired. Each possesses a three-layered membrane, a thick, brownish, smooth exospore, thin meso- and endospores (Fig. 99, 1). After a complete winter's rest, they germinate. They are finely granular, somewhat turbid, with a faveolate structure. The exospore ruptures and the endospore comes out, in *P. pachydermus* as a cylindrical, in *P. macrosporus* as a spherical sac (Fig. 99, 2). The vacuoles fuse to a large central vacuole and the protoplasm lines the wall as a homogeneous layer (Fig. 99, 3); probably nuclear divisions take place in it. By radial fissures, the wall layer is divided into uninucleate portions (spore mother cells) which, after two simultaneous nuclear divisions, separate into four spores each (Fig. 99, 4 to 7). At the top of the sporangium these gradually form a ball which, at the rupture of the sporangium, is shot off a short distance (Fig. 99, 8 to 10).

The spores are ellipsoidal, hyaline and uninucleate. Directly after they are ejected from the sporangium, they are connected by a small process and copulate (Fig. 99, 11 and 12). The nuclei enter the bridge

and whether they join in pairs or fuse has not been determined on account of technical difficulties. Hereupon they grow in nutrient solutions to a large sprout mycelium whose cells cling together (Fig. 99, 13 and 14). When they reach the host they put forth germ tubes between the epidermal cells into the interior.

The other species correspond to *P. macrosporus*, only in *P. inundatus* on *Apium graveolens*, the chlamydospores are differentiated into summer

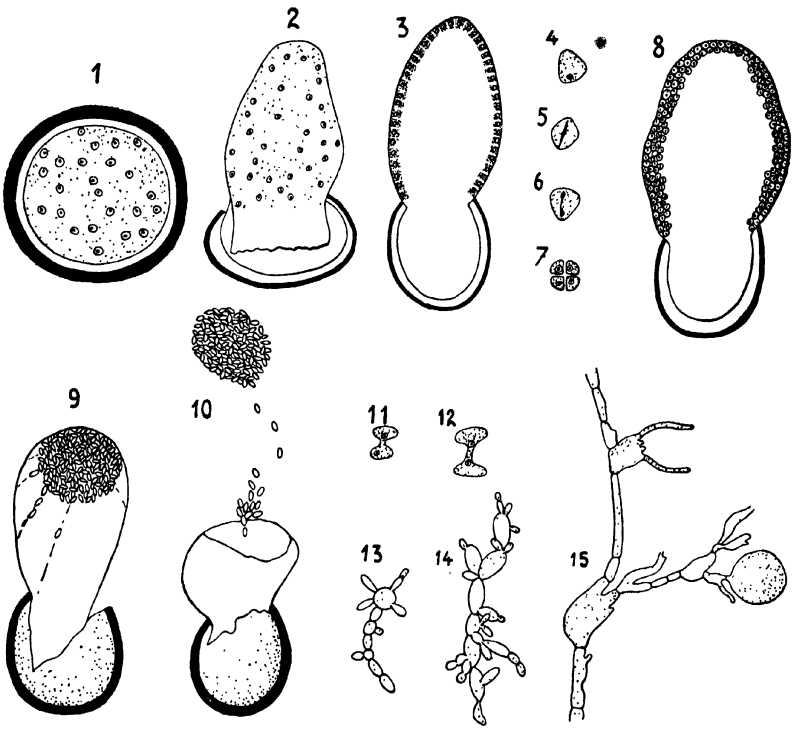


FIG. 99.—*Protomyces pachydermus*. 1 to 3, 8, 9. *P. macrosporus*. 4 to 7, 10 to 15. 1 to 10. Germination of hypnospores. 11 to 14. Copulation and development of endospores. 15. Young hypha with hypnospores. (1 × 540; 2, 3, 11, 12 × 670; 4 to 7 × 1,500; 8 × 520; 9, 10 × 300; 15 × 170; *after Meyer*, 1888, *and Büren*, 1915, 1922.)

and hypnospores. The summer spores germinate immediately after formation; in them the endospore does not come out, however, but degenerates in the interior of the chlamydospores into single endospores. In the hypnospores, which only germinate after a winter's rest, germination proceeds as in *P. macrosporus* (Dangeard, 1906; Büren, 1918).

A second genus, *Taphridium* (*Volkartia*), differs from *Protomyces* in that the chlamydospores are not formed irregularly in the deeper tissues of the host but as a continuous layer under the epidermis. In the forms

with exogenous germination, as *T. umbelliferarum* on *Heracleum* and *Peucedanum* and *T. Rhaeticum* on *Crepis*, the germ tubes (like the asci of *Taphrina*) stand beside each other like a hymenium. The endospores develop in a still unknown manner and fill the mature sporangium. In both species, the chlamydospores are capable of immediate germination; in the former, the mycelium winters over in the rhizome (Büren, 1917; Juel, 1921). An explanation of the life cycle of the Protomycetaceae from the point of view of change of nuclear phase is impossible at present, as the nuclear behavior is not clear. From an analogy to the Taphrinaceae and Ustilaginales, one might suppose that the dicaryon results from the copulation of the spores and the mycelium in the host belongs to the dicaryophase. Caryogamy would then occur in the chlamydospores before germination.

The position of meiosis is still uncertain in this scheme. Büren (1915) seeks it in the "tetrad-formation!" of the spore mother cells; hence he is forced to consider the spore mother cells as naked asci and the resulting endospore tube as a complex structure, a synascus, which is an entirely isolated structure in the fungi. If one wishes to avoid this explanation, one must assume that the quartering of the spore mother cells does not have the significance of a meiosis and that the spore mother cells, like the protospores of the Mucoraceae and Synchtriaceae, represent only an intermediate stage not connected with change of nuclear phase. Meiosis then, as in the Dipodascaceae and Endomycetaceae, would be sought in connection with the nuclear fusion in the beginning of nuclear divisions (not clearly demonstrated for *Protomyces pachydermus* and *P. macrosporus* but very probable from the observation of Fig. 99, 2 and 3) at the emergence of the endospore. Like the ascus of *Dipodascus*, the endospore would correspond to an ordinary ascus with still definite sporangial character, but encysted like the zeugites of many parasitic Basidiomycetes. Because of these uncertainties, the systematic position of this family is doubtful.

Taphrinaceae.—As a representative of this family may be cited *Taphrina deformans*, which causes serious damage to peach trees in Europe and North America. (Dangeard, 1894; 1896; Eftimiu 1927.) Its hyphae consist of binucleate cells which winter over in the bark, in the pith and in the medullary rays of the year-old twigs. In the spring, they penetrate the leaves emerging from the buds, spread rapidly and stimulate these to the formation of wrinkles by unequal growth. Eventually they force their way between the epidermal cells of the upper surface and form a reticulate tissue between epidermis and cuticle. The individual cells swell during nuclear fusion (Fig. 100, 1), round off, thicken their walls slightly, forming between epidermis and cuticle a compact layer of chlamydospores (Fig. 100, 2) capable of immediate germination. The exospore is ruptured and the endospore with the

protoplasm bulges out as a papilla, rupturing the cuticle. When the chlamydospores become entirely empty, the protoplasmic portion is abjointed from the vacuolate portion (Fig. 101, 1). This apical cell forms the young ascus; the vacuolate chlamydospore is called the stipe cell (in systematic literature).

The young ascus (Fig. 102, 5) contains a large diploid nucleus formed by the fusion of two hyphal nuclei during the formation of the chlamydospore. This nucleus divides thrice. In the first division, the spindle is generally transverse and here meiosis occurs. The protoplasm is in a peripheral wall layer, which is denser near the nucleus (Fig. 102, 8). The developing spores lie imbedded in a meager periplasm. In water, or sugar solutions, they develop sprout mycelia like yeasts; occasionally sprouting begins in the ascus, which then becomes filled by a dense sprout mycelium (Fig. 101, 4). In certain forms, young, still sporeless asci may develop vegetatively either to hyphae or sprout mycelia (Fig. 101, 2). These sprout mycelia are apparently biological substitutes for conidia since they fulfil the functions of propagation.

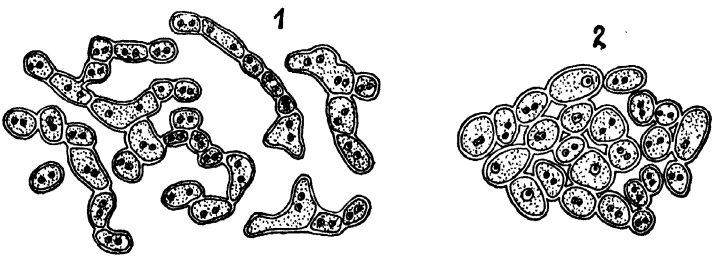


FIG. 100.—*Taphrina deformans*. 1. Subcuticular, binucleate ascogenous hyphae before caryogamy. 2. Young chlamydospores. (*After Dangeard*, 1894.)

Thus the chlamydospores may be interpreted as zeugites, organs in which at the close of the dicaryophase, caryogamy occurs. In this sense they would be considered homologous to the probasidia and sclerobasidia of the Auriculariales, to the teliospores of the Uredinales and the smut spores of the Ustilaginales, and thus the conceptions to be discussed under the Basidiomycetes, concerning the differentiation of zeugite and the sporophores and the encysting of zeugites, would also be important for the Ascomycetes. Although the validity of this interpretation is not yet certain, with these reservations it may be useful. The position of plasmogamy in this life cycle is unknown. In analogy to the Protomycetaceae and Ustilaginales one would expect it in the sprout mycelium although copulation has not yet been observed there.

The other Taphrinaceae follow, as far as known, the development of *Taphrina deformans*. In *Taphrina bullata* on pears and quinces, however, several dicaryons instead of one are present in the hyphae, but the mycelium becomes binucleate before spore formation.

The position and germination of the chlamydospores in the leaves of the host vary. In *T. epiphylla* on *Alnus incana*, (Juel 1921), *T. bullata* and *T. Betulae* (*Exoascus Betulae*) on *Betula alba* (Eftimiu 1927), the mycelium grows subcuticularly on the leaves and consequently the chlamydospores are formed between the epidermis and cuticle. In *T. aurea* on poplar, *T. Alni-incanae* and *T. Crataegi*, the mycelium appears just below the epidermis. In the majority of the Taphrinales, as in *T. deformans*, *T. institiae* and *T. Pruni*, the vegetative mycelium grows in the parenchyma while the ascogenous mycelium which forms the chlamydospores develops only under the cuticle. In *T.* (*Magnusiella*) *Potentillae*

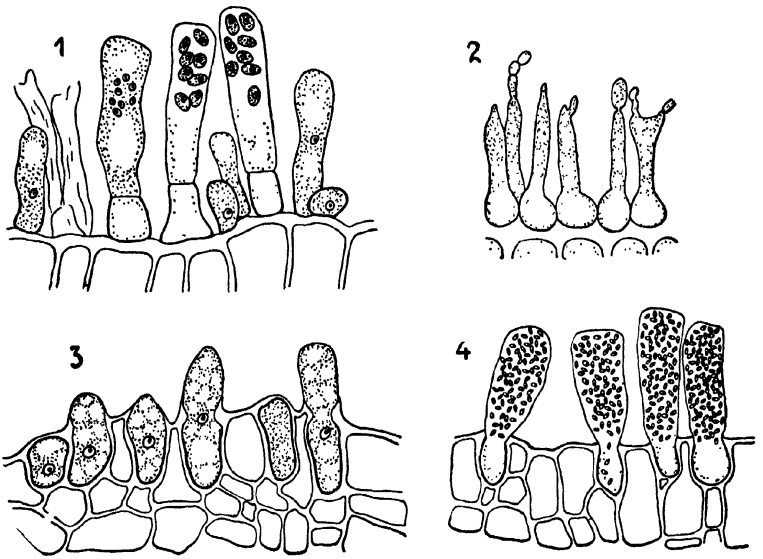


FIG. 101.—*Taphrina deformans*. 1. Hymenium (× 670). *Taphrina Carpini*. 2. Germination of asci in distilled water (× 400). *Taphrina aurea*. 3, 4. Hymenium (× 330). (*After Gwynne-Vaughan*, 1922, *and Sadebeck*, 1884.)

on *Potentilla*, the mycelium lives only in the interior of the leaves and the asci, as in *Taphridium* of the Protomycetaceae, are formed in a mycelial layer under the epidermis. In *T. aurea* on *Populus* and *T. epiphylla* on *Alnus*, the whole outer wall of the chlamydospores continues in the wall of the young ascus. There is no septum between ascus and chlamydospore, *i.e.*, no abjunction of a stipe cell (Fig. 101, 3 and 4; 102, 4). The types of germination of these forms are occasionally strikingly reminiscent of the Protomycetaceae. In *T. Coryli* on *Corylus americana*, the diploid nucleus divides into two daughter nuclei in the chlamydospore. One remains in the basal cell and degenerates; the other migrates into the young ascus and divides there into the 8 spore nuclei (Martin, 1924).

Because of this variation in the subordinate characters and the similarity of the more important characters, the systematic classification of the Taphrinales is confused. For a time, the forms with 4- or 8-spored asci were placed in *Exoascus*, the forms in which the germination of ascospores to sprout mycelium occurs in the asci in *Taphrina* (Sadebeck, 1884). This distinction has been shown untenable however, and consequently both genera must be united; for this the name *Taphrina* possesses priority. The forms in which the asci are not catenulate and intercalary, but single and terminal on branches which penetrate between the epidermal cells, are occasionally placed in *Magnusiella:* thus the

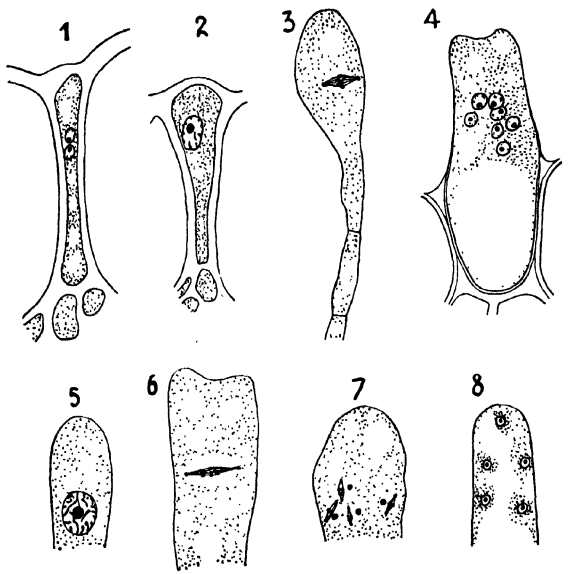


FIG. 102.—*Taphrina Potentillae.* 1 to 3. Development of ascus. *Taphrina epiphylla.* 4. Ascus before spore formation. *Taphrina Pruni.* 5 to 8. Development of ascus. (1, 2, 5, 6 × 1,000; 3, 7, 8 × 1,265; 4 × 670; *after Juel,* 1921.)

mycelium of *T.* (*Magnusiella*) *Potentillae* forms a continuous layer under the epidermis; from these there rise to the surface, between the epidermal cells, hyphal branches which grow toward the cuticle, each changing its end to an ascus (Fig. 102, 1 to 3). True chlamydospores are not formed in this case; this genus, however, is connected directly with *Taphrina* by transitional forms.

At present the Taphrinales include only parasitic forms which only recently have been demonstrated cultivatable in artificial media (Martin 1925), and which mainly occur in temperate zones, rarely in the tropics. They are specialized on three groups of cormophytes in three lines which are more or less sharply distinguished by the form of their asci (Giesen-

hagen, 1895). The first line, with clavate asci on ferns, has not been carefully studied. The second line with blunt, cylindrical asci more or less flattened at the top, on Amentiferae, includes *T. Tosquineti* on the leaves and female catkins of *Alnus*, *T. aurea* which causes saccate protrusions on leaves of *Populus* and forms yellow hymenia on their concave lower surfaces, and *T. Carpini* which stimulates the twigs of *Carpinus betulus* to the formation of witches' brooms. A third line with clavate to narrow cylindrical asci more or less rounded at the top, on Rosaceae, includes numerous species important in phytopathology, as *T. Pruni*, *T. institiae* and *T. Cerasi* on Prunus. The hyphae of *T. Pruni* live in the branches of plums and at flowering grow into the young fruits which undergo an abnormal development. Instead of forming a stone and outer fleshy layer, the fruit wall assumes a waxy, coriaceous character, and the whole fruit is a deformed, unpalatable structure. In these, the hyphae come out between the epidermal cells and branch between epidermis and cuticle to such a degree that the whole fruit is covered by ramose short-celled hyphae which subsequently become chlamydospores. *T. institiae* on plum and *T. Cerasi* on cherry stimulate the host to the formation of witches' brooms; *T. deformans* causes leaf curl of the peach.

The Taphrinaceae show relationships to the Protomycetaceae. As in the latter, intercalary chlamydospores are formed on the mycelium, singly in the Protomycetaceae, serially in the Taphrinaceae. As in the Protomycetaceae, these chlamydospores germinate with an ascus; only in most Protomycetaceae the endospore separates from the exospore, while their connection continues in the Taphrinales. The separation of the ascus from the stipe cell, regarded in this light, might be considered as a subsequent device to prevent the retreat of the protoplasm. In both families the ascospores arise in a protoplasmic peripheral layer; in *Taphrina* the chlamydospore generally shows a simple zygote, in *Protomyces* (if this interpretation is permissible) a coenozygote, and, as in the Protomycetaceae, the ascospores germinate to a sprout mycelium.

Which of these families may be considered as primitive and which derived, and whence their derivation, is still obscure. The simplest form so far investigated is *T.* (*Magnusiella*) *Potentillae* which lacks true chlamydospores; whether it is next the ancestral form, may not be determined at present. In any case, the Taphrinaceae form a very old family, as may be concluded from their biological relationships, especially from their adaptation to hosts.

CHAPTER XIII.

EUASCOMYCETES

The Euascomycetes differ from the Hemiascomycetes in that the zygotes develop first to ascogenous hyphae which then proceed to the formation of asci. Parellel with this formation of ascogenous hyphae, there generally develops ascigerous fructifications whose morphological relationships form the basis of the systematic classification of this subclass.

Originally the Euascomycetes were divided into four orders which may be regarded as the four historical orders, the Pyrenomycetes with perithecia, the Discomycetes with apothecia, the Tuberales with hypogaeous tuberiform fructifications and the entomophilous Laboulbeniales with a modification of the perithecia. Recently the Pyrenomycetes, and Discomycetes have been extensively subdivided on the basis of the manner of opening of the fructifications and the arrangement of the asci. The cleistocarpous Pyrenomycetes, in which the ascospores are only liberated by a decay of the perithecia, are assembled in the Plectascales Perisporiales and Myriangiales. The higher Pyrenomycetes, however, in which generally the liberation or discharge of ascospores is facilitated or made possible by the formation of a special opening, are grouped in the Hypocreales, Sphaeriales, Dothideales, Hysteriales and Hemisphaeriales. The Discomycetes are divided into the Phacidiales, in which the apothecial covering is only ruptured at maturity, and the Pezizales, in which it is generally reduced to threads during the development of the apothecia. Thus in the classification followed here the Euascomycetes include 12 orders whose characters will appear in the course of the discussion and whose probable morphological relations are graphically represented in the collective scheme at the close of the book (p. 618).

PLECTASCALES

Among the typical Ascomycetes the Plectascales are characterized by the possession of angiocarpous perithecia without ostioles, whose interior is irregularly penetrated by ascogenous hyphae, consequently the asci (generally spherical) lie scattered irregularly in the ground tissue of the fructification. The peripheral layers of the fructifications may thicken to a pseudoparenchymatous rind which, in the lower forms, gradually degenerates at maturity.

The forms of the Plectascales to be discussed here fall into six families: the Gymnoascaceae, Aspergillaceae, Onygenaceae, Trichocomaceae, Terfeziaceae and Elaphomycetaceae. The Gymnoascaceae and Aspergillaceae have simple perithecia, without or with a loose pseudoparenchy-

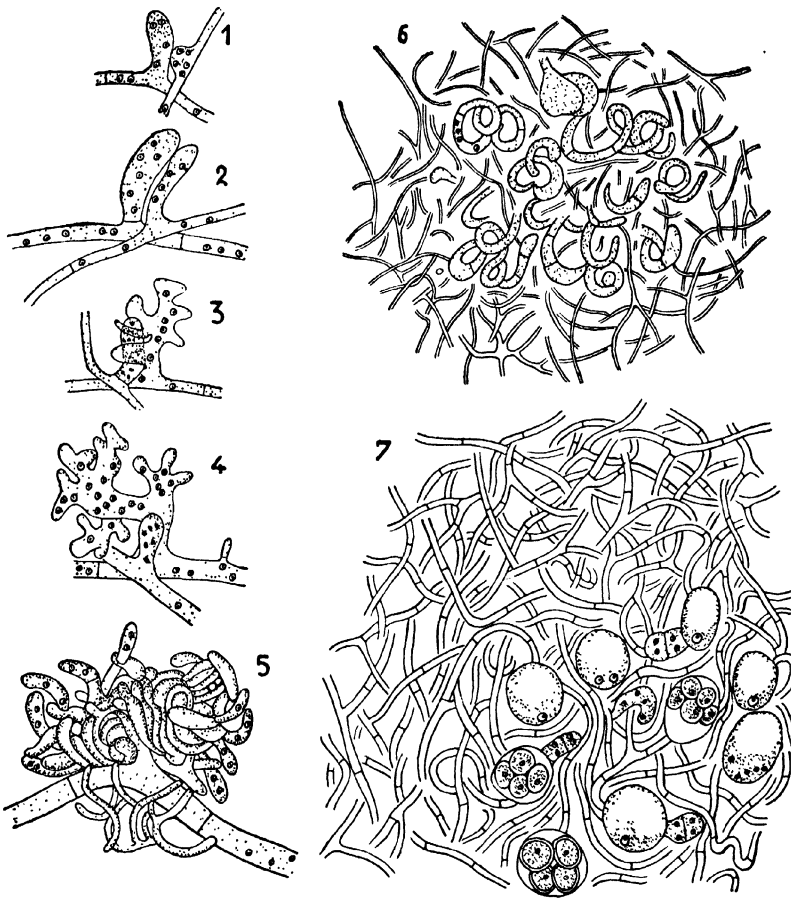


FIG. 103.—*Amauroascus verrucosus*. 1, 2. Fundaments of copulation branches. 3, 4. Ascogonium develops parthenogenetically, while nuclei degenerate in antheridium. 5. Knot of ascogenous hyphae being surrounded by sterile hyphae. 6. Young perithecium with ascogenous hyphae. 7. Older stage with young asci. (× 600; *after Dangeard*, 1907.)

matous peridium. In the highest representatives of the second family, the perithecia develop to complicated structures which are divided by sterile veins into ascogenous nests.

The third to sixth family include high forms with complicated and much differentiated fructifications. In the Onygenaceae and Trichoco-

maceae, they are divided into sterile stipes and fertile heads. In the Trichocomaceae, the sterile veins have intertwined to faveolate structures open at the top. In the Terfeziaceae and Elaphomycetaceae, they have developed to truffle-like, hypogaeous structures which in the former are soft and degenerate as a whole, in the latter surrounded by hard, resistent peridium, the gleba breaking down into a dusty spore mass with capillitium.

The diagrammatic representation of the morphological relationships between these families is given in the summary at the close of the order.

Gymnoascaceae.—The simplest member of this group to be studied cytologically, *Amauroascus verrucosus* (Dangeard, 1907), is generally closely connected to *Eremascus*. On its substrate, garbage and dung, it forms a white arachnoid covering which thickens in places to small white knobs, the fundaments of fructifications. From any two hyphae multinucleate copulation branches are formed and basally abjointed (Fig. 103,

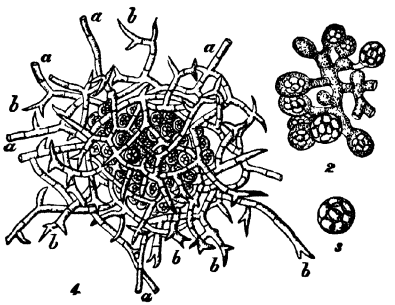


FIG. 104.—*Gymnoascus Reessii*. 1. Small fructification; *a*, vegetative hyphae. *b*, loose peridium which surrounds the ascigerous tissue. 2. Group of asci. 3. Mature ascus. *After Brefeld*, 1891 *and Baranetzky*, 1872.)

1 and 2). One branch, the antheridium, is vertical and somewhat the stronger; the other, the ascogonium, is somewhat slenderer and is coiled around the antheridium in a helix. A solution of the separating wall at the tip of both organs and nuclear migration has not yet been observed. The ascogonium continues its growth and branches often (Fig. 103, 3 and 4). The branches coil spirally (Fig. 103, 5) and after a certain time divide into binucleate cells which swell to eight-spored asci (Fig. 103, 6 and 7).

Meanwhile this knob of ascogenous nyphae is surrounded by a compact, sterile, hyphal tissue, so that the asci are imbedded in a loose brownish hyphal cushion, which is the simplest form of a fructification (perithecium).

In *Gymnoascus* the hyphal sheath possesses a more marked peridial character. *Gymnoascus* is saprophytic on earth, on offal, dung, cadavers, etc., and forms a fluffy, occasionally brightly colored, covering on the

substrate. The hyphae are slender and divided into short multinucleate cells; in some species, as *G. setosus*, they laterally abjoint hyaline conidia which may grow further by sprouting; in other species, as *G. uncinatus*, they may break up into oidia. In *G. Reessii* imperfect forms are unknown and reproduction takes place only sexually by perithecial formation.

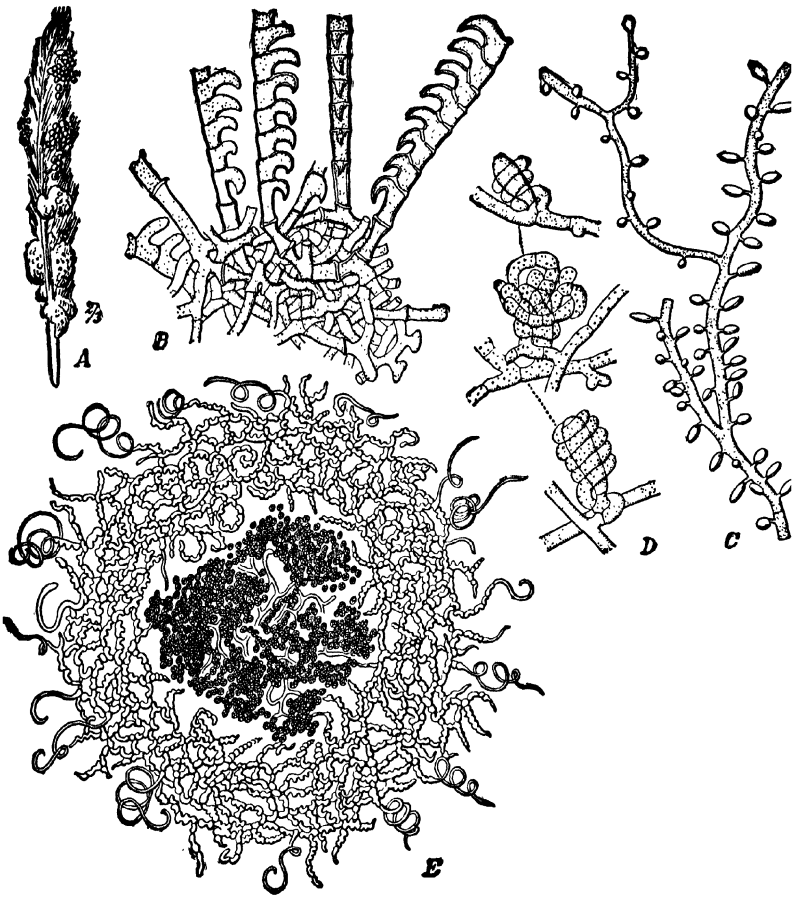


FIG. 105.—*Ctenomyces serratus*. *A*. Feather covered with fungus. *B*. Resting mycelium with pectinate organs. *C*. Vegetative hyphae with conidia. *D*. Copulation branches. *E*. Section of mature fructification. (*A* × ⅔; *B* to *D* × 400; *E* × 200; *after Eidam*, 1883.)

As in *Amaurascus verrucosus*, each of two neighboring cells of a hypha (as in *G. Reessii*) or two different hyphae (as usually in *G. candidus*) forms a copulation process which is abjointed. Generally both branches appear simultaneously; occasionally the antheridium appears somewhat earlier,

As in *Amauroascus*, the ascogonium winds helically around the antheridium; in contrast to *Amauroascus*, the separating wall at the tip is dissolved and the male nucleus migrates into the ascogonium. This is divided by septa into binucleate (?) cells which develop to ascogenous hyphae on which arise, terminally or laterally, the eight-spored asci. Meanwhile the sexual organs have become surrounded by a loose hyphal tissue (Fig. 104, 1) whose peripheral hyphae form peculiar lateral spines and whose membranes thicken and turn brown at maturity (Eidam, 1883; Dale, 1903).

The most compactly built rind is found in *Ctenomyces*. Its only well-known species, *C. serratus*, found on decaying feathers in henyards, forms hyphal tissue, hyaline when young, whose hyphae abjoint laterally numerous oval hyaline conidia. The cells of the hyphae are 1 to 4 nucleate, the conidia (Fig. 105, *C*) are generally uninucleate. The conidiophore hyphae may branch in fascicles and may finally come together to pycnidia-like masses in which the conidiophore hyphae later swell, filling the cavity with a slimy conidial mass.

The young copulation branches are 1 to 3 nucleate, the male branch develops to a vertical clavate structure which finally contains 10 to 12 nuclei (Fig. 105, *D*). The ascogonium winds 6 to 7 times about the antheridium and finally contains about 20 nuclei. A solution of the separating wall and nuclear migration has not been observed. Without further processes the ascogonium divides into binucleate almost isodiametric cells; these develop to ascogenous hyphae which again coil helically and surround the original helix. From this confusion, the eight-spored asci arise in an unknown manner. Meanwhile the whole knob is closely surrounded by sterile hyphae which, with considerable thickening of their walls, become moniliform and partly develop on one side to peculiar short processes.

Besides these perithecia, light brown sclerotia are also formed on the feathers. The cells in the vicinity of the septa are nodose (Fig. 105, *B*). From these there arise unusual pectinate, falcate or setiform hyphae, whose unguiform processes are turned in the same direction. Possibly they serve to disseminate the sclerotia by clinging to foreign bodies (Eidam, 1883; Matruchot and Dassonville, 1899; Dangeard, 1907). These falcate and other structures of *Ctenomyces* are strikingly reminiscent of certain imperfect genera, as *Trichophyton*, *Microsporum* and *Achorion*, which cause ringworm, favus and other skin and hair diseases in men and animals. It has become probable through the investigations of Matruchot and Dassonville (1899*a*, 1901; Grigoraki, 1925) and others that these imperfect genera belong to the Gymnoascaceae, *i.e.*, to *Ctenomyces* and the closely related *Eidamella*.

Aspergillaceae.—The simplest member of the Aspergillaceae, *Aphanoascus cinnabarinus*, is directly connected to the Gymnoascaceae. Like

most Gymnoascaceae, it is found on decaying feathers and dung. The cells are multinucleate. As in *Gymnoascus setosus* and *Ctenomyces serratus*, they abjoint lateral or terminal, hyaline, oval, multinucleate conidia. The formation of the perithecium takes place as in the Gymnoascaceae. The copulation branches arise from neighboring cells of the same hypha or two separate hyphae. From the first, they are multinucleate and subsequently undergo several nuclear divisions. The ascogonium is slender and lies as a helix around the spherical antheridium (Fig. 106, 1). Fertilization is absent; the male nuclei degenerate; the ascogonium develops parthenogenetically. As in *Ctenomyces serratus*,

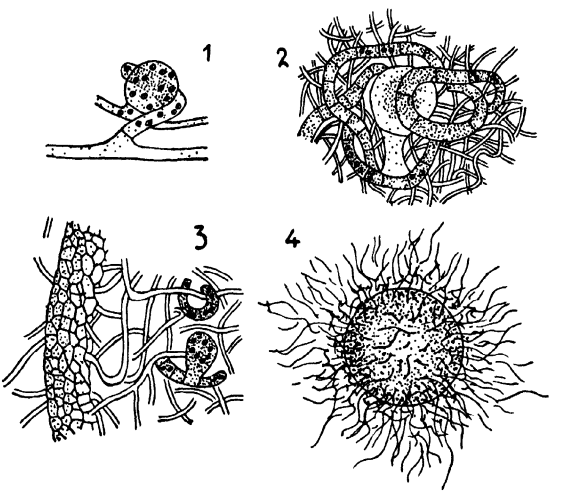


FIG. 106.—*Aphanoascus cinnabarinus*. 1. Small ascogonium coils about spherical antheridium. 2. Ascogenous hyphae coil about antheridium whose contents are degenerating. 3. Section of periphery of an immature perithecium. The cells of the ascogenous hyphae are about to develop laterally to asci. 4. Mature fructification. (1 to 3 × 600; 4 × 10; *after Dangeard*, 1907.)

it divides into binucleate cells; some of these grow to ascogenous hyphae which coil helically and form lateral secondary branches which again coil helically. The whole system is abjointed into binucleate cells which apparently form the asci as lateral outgrowths (Fig. 106, 3). Meanwhile the knot is closely surrounded by sheath hyphae intertwining at the periphery into a pseudoparenchymatous wall of several layers. The perithecia are up to 2 mm. in diameter, hyaline at first, becoming yellowish brown and finally cinnabar red (Dangeard, 1907).

In *Aphanoascus* the peripheral layers of the rind form a definite pseudoparenchymatous peridium, while in the Gymnoascaceae they form a plectenchymatous tissue; *Aphanoascus*, thus, has been considered by

many authors a member of the Gymnoascaceae. The other genera of the Asperigillaceae may be divided into three radiating lines whose representatives will be discussed as the *Monascus–Magnusia*, the *Thielavia*, and the *Aspergillus–Penicillium* groups.

Monascus has been well investigated in two species, *M. purpureus* and *M. Barkeri*. Both were originally isolated from red Chinese rice but have since been found in silage and preserves (Buchanan, 1910; C. E. Lewis, 1910). As far as may be culled from conflicting accounts, (*e.g.*, Barker, 1903; Ikeno, 1903; Kuyper, 1905; Olive, 1905; Dangeard, 1907; Schikorra, 1909) the development is probably as follows: the mycelium consists of regularly branched hyphae which cut off singly, or basipetally in chains, spherical or pyriform conidia (Fig. 107, 1 *C*). Both the hyphal cells and conidia are multinucleate.

When the fructification develops, a four- to eight-nucleate terminal cell is abjointed and remains stationary in its development, becoming the antheridium. Directly under the septum, the ascogonial mother cell is

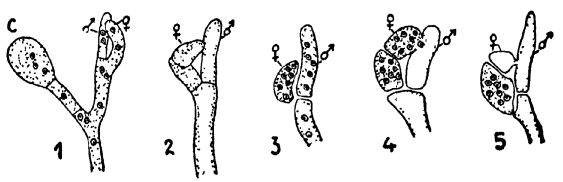


FIG. 107.—*Monascus purpureus*. Development of copulation branches. *C*, conidium. (1, 2 × 420; 3 × 725; 4, 5 × 835; *after Schikorra*, 1909.)

abjointed and coils helically about the antheridium. It is further divided into a three- to four-nucleate terminal cell, the trichogyne, and a four- to six-nucleate subterminal cell, the ascogonium. The nuclei of the trichogyne subsequently degenerate. Usually the antheridium forms a papilla toward the trichogyne, open communication results, and the male nuclei migrate into the trichogyne. Thereupon the wall between trichogyne and ascogonium is temporarily dissolved, the male nuclei migrate into the ascogonium, pair with the female nuclei, and migrate into the ascogenous hyphae. The antheridium collapses and disintegrates (Fig. 107, 3 to 5).

Meanwhile the cell group has become closely surrounded by sterile sheath hyphae which apparently nourish the swollen, spherical ascogonium and hence are gradually dissolved in the core of the fructification. The peripheral layers are brown and pseudoparenchymatous, forming the perithecial wall. The ascogenous hyphae divide (according to Dangeard); as in previous forms, into binucleate cells which swell into eight-spored asci. According to Schikorra, the development of the asci takes place according to the *Pyronema* type.

In *Monascus*, in contrast to *Aphanoascus* and the Gymnoascaceae, the female copulation branch no longer fulfils its original sexual function as a whole, but is divided into a receptive cell, the trichogyne, and the true female gametangium, the ascogonium.

This development continues characteristically in *Magnusia*, which extends much beyond *Monascus* both in the imperfect forms and the structure of sexual organs and perithecia. The only representative so far investigated, *Magnusia nitida*, in contrast to *Monascus*, has uninucleate cells (Satina, 1923). Its imperfect forms are reminiscent of tufts of *Penicillium* and under favorable nutritive conditions form coremia. The sexual apparatus consists of a unicellular antheridium, a helical ascogonium and a multicellular trichogyne; the latter grows toward the antheridium, embraces it, twines around it, comes into open connection and its content flows into the ascogonium. The latter develops ascogenous hyphae according to the hook type. The perithecia are shining black, ellipsoidal or irregularly angular; they have long spiral appendages deceptively like the appendages of the Erysiphaceae; only, in contrast to the latter, they do not arise from peripheral but from deeper cells and hence, in a certain sense, are formed endogenously.

As regards the morphology of the sexual organs, *Magnusia* is distinguished from *Monascus* by the spiral ascogonium, by the septation of the trichogyne and by the length of the latter which varies with the distance from the antheridium. This relationship offers an approach to the comprehension of several higher orders of Ascomycetes.

A second line is formed by *Thielavia* whose best-known representative, *T. basicola*, appears in damp weather on the roots of numerous phanerogams and in Europe and North America causes a serious root rot of tobacco. The mycelium penetrates the infected roots in all directions, and on their surfaces cuts off such a great mass of conidia that they seem to be covered by a mildew. Because of their peculiar manner of liberation, these conidia are called "endoconidia" by the phytopathologists (Brierly, 1915). A hypha forms a lateral outgrowth and the nucleus divides so that a daughter nucleus migrates into the daughter cell. The daughter cell is abjointed and elongates into a flask-shaped conidiophore (Fig. 108, 1) whose nucleus divides again. One daughter nucleus remains at the base, the other migrates toward the tip which is abjointed. Now the membrane of the terminal cell separates into an outer and inner layer; the outer ruptures at the top and the conidium gradually emerges (Fig. 108, 2). Meanwhile the nucleus of the basal cell divides and repeats the abjunction of the conidium. With every conidium, the sheath increases in length and finally a long row of conidia are enclosed in the sheath and slowly press outward. Thus these conidia are not endoconidia in the strict sense of the word, but ordinary acrogenous conidia which, however, have been freed from the mother plant by a peculiar mechanism of libera-

tion. This same manner of formation of conidia we will meet again in the following order in the Erysiphaceae, only there the spore membrane does not rupture.

With the progress of the disease, the conidia disappear and there appears on infected roots, a dark covering of brown, thick-walled gemmae (chlamydospores) which arise catenulately and are liberated as the hyphae disintegrate (Fig. 108, 3). Later, when the roots are dead, there appear shining black perithecia whose ontogeny and whose connection with both imperfect forms has not been experimentally investigated.

While the *Thielavia* group shows a strong development of conidial apparatus, this reaches its maximum in the third line, the *Aspergillus–Penicillium* group. The representatives of this group are cosmopolitan and the most common of all fungi. In them, also, various groups of

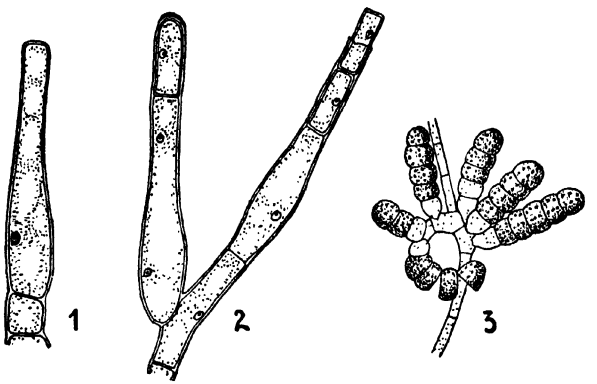


FIG. 108.—*Thielavia basicola*. 1. Young conidiophore before the formation of the first conidium. 2. Older stage. The left branch has formed the wall of the first conidium; the basal cell is again binucleate. The right branch shows the first conidium leaving the sheath. 3. Chlamydospores. (× 500; *after Brierly*, 1915.)

species vary in their ecological characters. Thus the true species of *Penicillium* occur in forest floors, more rarely on cultivated, manured ground as mesosaprobes on which bacteria preponderate. In forests they are more important than the Mucoraceae, and by the digestion of hemicelluloses play an important role. In addition, they occur in temperate climates on garbage and offal. In the tropics, the species of *Aspergillus* predominate and there colonize everything possible.

Many species of this group are technically important on account of their hydrolytic powers on starch, sugars and tannins and cause fermentations to oxalic, citric, and gallic acids, more rarely to alcohol, as *Aspergillus Oryzae* which is used in Japan in the preparation of sake (rice wine) and soy bean sauces by the hydrolysis of starch. In America, the diastase from this organism is widely used instead of malt diastase in industry; *Aspergillus Wentii*, by the loosening of the hard tissue of the

bean, assists in the preparation of the soy bean as used in Java; several species of *Citromyces* are used in citric acid fermentation; *Penicillium roqueforti* and *P. camemberti* lend to the corresponding cheeses their characteristic aroma and consistency. Some species whose optimal temperature is about 37° are pathogenic to animals and cause mycoses; *Aspergillus fumigatus* and *A. flavus* grow in the human ear and the former causes most of the cases diagnosed as tuberculosis, in which *Mycobacterium tuberculosis* is not found. Still other species are plant pathogens, thus *P. italicum* and *P. digitatum* (*P. olivaceum*) cause decay of ripe southern fruits, and *A. niger* is said to be parasitic in dates and make them unpalatable by fermentation of the starch.

The thallus is formed as in the previous groups. It is generally colorless; in some species the hyphae may form in the interior of the cells

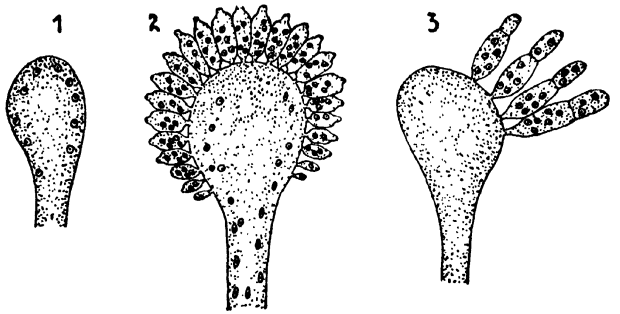


FIG. 109.—*Aspergillus herbariorum*. Development of conidiophore. (× 600; *after Dangeard*, 1907.)

a yellow to red, rarely green, color which later diffuses through the cell membrane and passes out into the nutritive solution. Exceptionally, as in *Penicillium camemberti*, the hyphae may break up into oidia or, again in *Scopulariopsis* sp., form gemmae or, as in *Aspergillus niger* or *A. Oryzae* (Schramm, 1914; Zikes, 1922), develop sprout mycelia. The hyphae form an arachnoid cover over the substrate and interwine rapidly into a dense mat or crust. This is generally white at first and after a few days attains its characteristic color from its conidia.

As imperfect forms, in addition to the above-mentioned oidia, only conidiophores and conidia have been known. The conidiophores arise only on the surface of the mycelium as vertical, projecting, aerial hyphae. In the simplest case, as in *Aspergillus*, they are unbranched; as in *Syncephalastrum* among the Mucoraceae, their ends swell capitately and allow the majority of the nuclei to come out into short flask-shaped **phialides** (sterigmata) which cut off successively a chain of multinucleate conidia (Fig. 109). While in the typical species of *Aspergillus*, the phialides are unbranched (Fig. 114, *A*), in the subgenus *Sterigmato-*

cystis, they branch repeatedly (Fig. 116, 1 and 2). In the only cytologically studied species belonging to this subgenus, the phialides, and hence the conidia, are uninucleate.

From *Aspergillus*, *Aspergillopsis* and *Citromyces* form an unnoticeable transition to the second important genus whose conidiophores are much branched and lack the capitate swellings at the junction of phia-

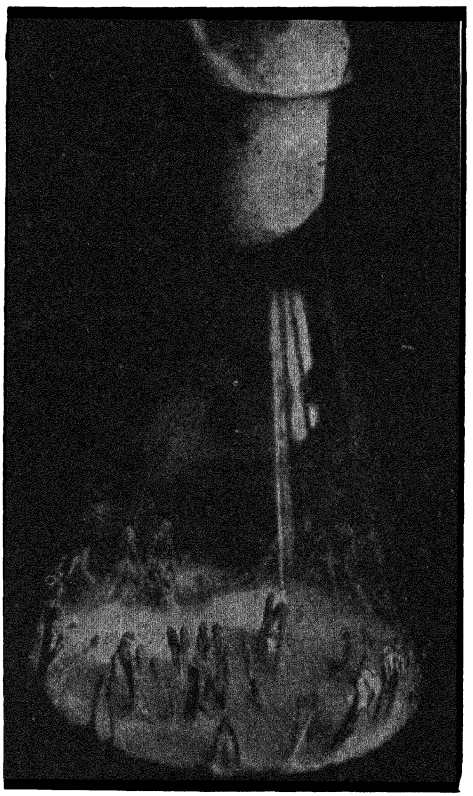


FIG. 110.—*Penicillium claviforme*. Coremia on malt agar, with snowy aerial mycelium. (*After Wehmer*, 1914.)

lides (Fig. 117, *B*). The outermost branches from which the phialides radiate have a certain systematic value and are called **metulae** (Westling, 1911). While in the majority of forms the metulae and phialides (like the hyphal cells) have several nuclei, in some strains of the *Penicillium crustaceum* group, as in *Aspergillus* (*Sterigmatocystis*) *nidulans*, they are uninucleate; in these forms on a thallus with multinucleate cells there arise uninucleate conidia which only at germination again become multinucleate.

In many species, the conidia are bound together in chains by short disjunctors (connectives). Brefeld (1874) regards this in his *Penicillium "crustaceum"* as a section of the "sterigma." Thom (1914; Thom and Church, 1926) considers that in *Aspergillus* the true, thick, round spore wall has only arisen in the cells cut off from the phialides; in case these original cells are not entirely filled out, the collapsed residue remains hanging as a connective between the spores. According to some observations of the author on *Penicilliopsis clavariaeformis* it is a question of papilliform arching at the base of the conidia whose function is still unknown.

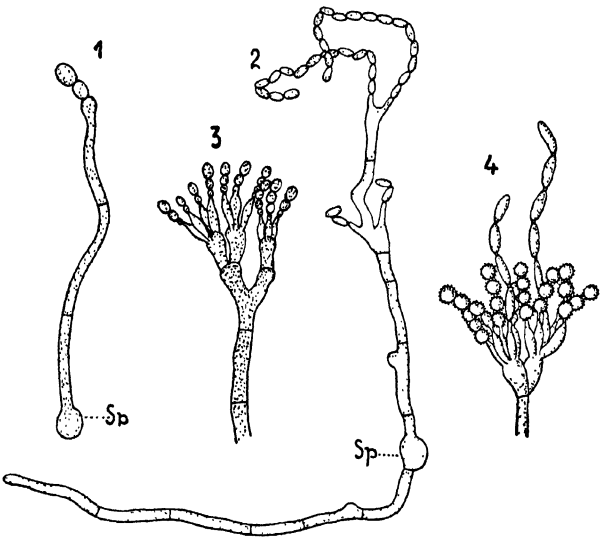


FIG. 111.—*Penicilliopsis clavariaeformis*. 1 to 3. Development of the conidiophore. *Sp*, germinated conidium. *Penicilliopsis brasiliensis*. 4. Conidiophore with dimorphic conidia. (× 330; 1 to 3 original; 4 *after Möller*, 1901.)

Under certain cultural conditions, as on substrates which contain nitrogen in the form of nitrates, also by increased transpiration, by lowering the oxygen tension of the air, in the presence of glycerol as a carbon source, or in definite physical state of the substrate, the conidiophores of many species of *Penicillium* form coremia (Munk, 1912; Wehmer, 1914; Boas, 1915, 1916). While these coremia (Fig. 110) in true species of *Penicillium* form only as abnormalities, in some other genera (by some authors regarded as subgenera of *Penicillium*), as in *Acaulium* (Fig. 7, 2) and *Stysanus* (Fig. 7, 1), they have become the rule and thus arise normally. In these genera there are beginnings of conidial fructifications which we shall meet later in *Isaria* (imperfect forms of *Cordyceps*) under the Hypocreaceae; thus a series of species

fundamentally belonging in Aspergillaceae are placed in *Isaria* until their natural position has been determined on the basis of their perithecia.

These imperfect forms attain the highest development in the tropical genus *Penicilliopsis* of which two representatives, the Javan *P. clavariaeformis* (Solms-Laubach, 1886) and the Brazilian *P. brasiliensis* have been carefully investigated. If *P. clavariaeformis* is allowed to grow on a synthetic substrate, many undifferentiated hyphae after two days begin to cut off a long chain of hyaline oval conidia (Fig. 111, 1). In this respect they seem entirely like the conidial hyphae of *Monascus*. Later there appear on the mycelia true conidiophores (Fig. 111, 3) whose form is intermediate between *Penicillium* and *Aspergillus* and is

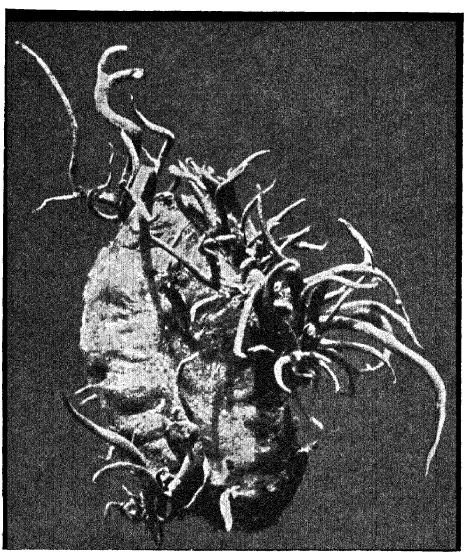


FIG. 112.—*Penicilliopsis clavariaeformis*. Coremia on fruits of *Diospyros macrophylla*.

reminiscent of *Citromyces caeruleus* and *C. purpurescens*. Their mycelium is an intense yellow. Later they collect into massive, plectenchymatous, antler-like coremia whose peripheral hyphae radiate perpendicularly to the outer surfaces and again degenerate to short stipitate conidiophores. They often swell capitately to a greater degree than is shown in Fig. 111, 3 for the free conidiophores and then seem deceptively like *Aspergillus*. The appearance of these coremia on the natural substrate (*Diospyros macrophylla*) is shown in Fig. 112; in artificial culture they may grow to 20 cm. In *P. brasiliensis* they are verticillately branched and generally reminiscent of *Araucaria*.

Conidia of the *Aspergillus–Penicillium* group are spherical or ovoid, smooth, rough or echinulate, hyaline or slightly colored. It is their

masses which give the hyphal mats their characteristic tint. This tint, however, as well as the size of the conidia, varies considerably according to the nourishment, temperature and physical character of the substrate. Thus *P. candidum* forms on paper and on acid substrates a white strain with white conidia just as almost all *Penicilia* form a white or light red color on paper. If the same species grows on alkaline or protein substrates, the mycelium is dark, almost black and forms no perithecia. On carbohydrate substrates, it forms, if we may anticipate our discussion, carbonaceous perithecia which together form a hard shining mass. When the perithecia are emptied, the ascospores give these carbonaceous masses a mealy, flabby, lustreless appearance and a coffee-brown color. That variations of this sort, especially if they are caused by the presence of toxic agents or experimental interference, can remain constant through a long series of generations has been shown by Haenicke (1916) and others. At germination, the conidia swell to three times their original size and put forth several germ tubes which develop multi septate, and branched mycelium. An exception to all these forms is *Penicilliopsis brasiliensis* in which on the same conidiophores there are formed ellipsoid smooth and spherical verrucose conidia (Fig. 111, 4). The physiological nutritive conditions and biological significance of this dimorphism is still unknown.

As the imperfect forms of the Aspergillaceae are the forms ordinarily seen and since the physiological nutritive characters of the mycelium offer very important diagnostic characters in their relation to citric acid, tannins and arsenic compounds, they have been repeatedly monographed (Wehmer, 1901; Westling, 1911; Sopp, 1912; Thom and Church, 1921, 1926; Biourge, 1923). As has been already mentioned, many forms are considerably modified by the substrate and a single description to enable later identification is often almost impossible; thus in forms described as *Penicillium glaucum* and *P. crustaceum*, extensive physiological investigations do not determine what the various authors really had in hand.

The perithecia correspond with the perithecia of other Aspergillaceae. They are generally formed on the mycelial mats, with rapid transpiration, and begin to appear about 1 to 2 weeks after the inoculation of the cultures. The laws governing their appearance are still unknown. Brefeld (1874) assumes for *Penicillium "crustaceum"* an absence of oxygen as a fundamental condition; Bezsonov (1919) shows for *P. "crustaceum," Aspergillus Oryzae* and *A. Wentii* that a high sucrose content favors their formation.

With the exception of *Penicilliopsis*, in all species so far studied, their formation is preceded by the formation of sexual organs. The process taking place may be briefly discussed in five groups. In the first group, as in *Penicillium Brefeldianum* (*P. "crustaceum"* Brefeld, 1874) and

in *Aspergillus nidulans* (Eidam, 1883; Dangeard, 1907), as in *Eremascus*, two equal copulation branches are formed; they coil around each other helically (Fig. 117, *C*) and apparently come into open communication at the tip. The content of one branch migrates into the other. Both copulation branches are then surrounded by a dense hyphal knot (Fig. 117 *D*), which subsequently assumes a plectenchymatous character. Thus in these forms antheridium and ascogonium are still equivalent and may be directly ranked with the equally isogamous copulation branches of many Endomycetaceae and Gymnoascaceae.

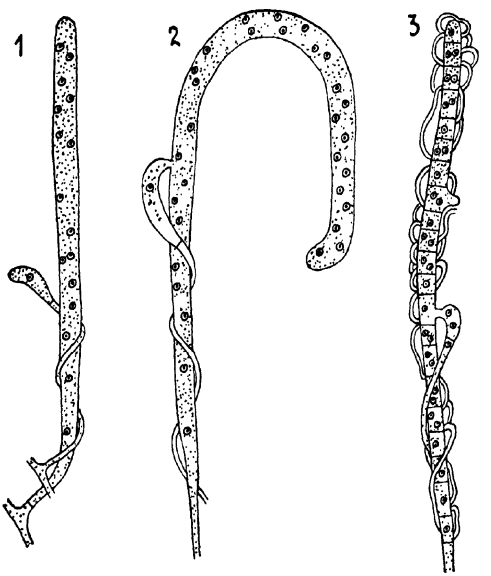


FIG. 113.—*Penicillium Wortmanni*. 1. The multinucleate ascogonium and young antheridium. 2. The antheridium is in open communication with the ascogonium but the male nucleus remains in the antheridium. 3. The ascogonium surrounded by sterile hyphae is divided into binucleate cells which are beginning to develop ascogenous hyphae. (× 600; *after Dangeard*, 1907.)

In a second group, which includes only *Penicillium Wortmanni* (*P. vermiculatum*) (Dangeard, 1907), the copulation branches, as in *P. "crustaceum,"* are arranged regularly; however, they show a characteristic differentiation in their behavior. In this species the hyphae are always uninucleate. On the formation of the perithecium there appears, as a branch of any hypha, a unicellular ascogonium rich in protoplasm, which, like the other cells of the hypha, contains a single nucleus. It elongates rapidly and by repeated nuclear division becomes as much as 16-nucleate. Meanwhile there has appeared a second slender branch, the young antheridium. Generally it arises from a different hypha than that which

bears the ascogonium. It winds several times around the ascogonium and cuts off a uninucleate apical cell which swells slightly (Fig. 113, 1).

Meanwhile the number of nuclei in the ascogonium have reached about 64. The apical cell comes into open communication with the ascogonium (Fig. 113, 2). Dangeard could not see nuclear migration, however, and concluded that the male nucleus remains in the antheridium

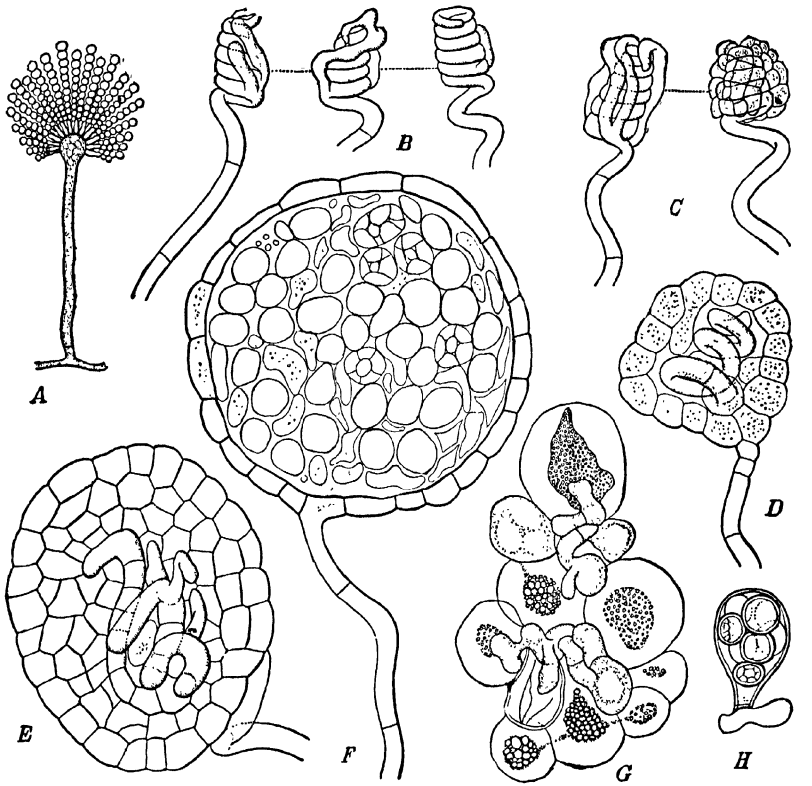


FIG. 114.—*Aspergillus herbariorum*. *A*. Conidiophore. *B* to *F*. Development of perithecium. *G*. Group of young asci. *H*. Mature ascus. (*After Kny and Bary.*)

and degenerates. The ascogonium divides into numerous binucleate cells, however, each of which may develop ascogenous hyphae (Fig. 113, 3).

Thus *P. Wortmanni* differs from *P. crustaceum* in two respects. Both copulation branches are differentiated morphologically as well as dynamically into antheridium and ascogonium; secondly, the appearance of the antheridium is retarded. It appears a long time after the formation of the ascogonium, when the latter has already become multinucleate,

and, if Dangeard observed the normal development, its single nucleus is functionless.

The behavior of the third stage will be described for the best-known *Aspergillus herbariorum–repens* group. (For *A. herbariorum*, by investigations of Fraser and Chambers, 1907, and Dangeard, 1907, and for *A. repens*, a small variety of *A. herbariorum*, by the investigations of Dale, 1909 and Moreau, 1913). As a branch of a hypha, there arises an ascogonium, which coils in a helix with a continually shortening radius. It is divided by one or more septa in two or more multinucleate cells of which the terminal is generally the longest and contains up to 20 nuclei. Shortly before or after septation of the ascogonium, the antheridium appears and climbs along the ascogonial helix (Fig. 114, *B*, *C*). Many times it is formed independently of the ascogonium, on another hypha, often it grows from two or three slender branches on the basal, more rarely from a higher coil of the ascogonium; occasionally it may arise from the interior of the helix and thereby attain the same aspect as in *Aphanoascus* and *Ctenomyces*. An open communication between antheridium and ascogonium was not demonstrated in any case. The antheridium appears to be rudimentary; the nuclei often degenerate before it has reached its full length, or it ceases its growth half way and does not reach the tip of the ascogonial spiral; or it may be entirely absent. In all these cases, with or without the antheridium, the ascogonium develops parthenogenetically; it divides into binucleate cells some of which grow to ramose ascogenous hyphae.

Thus the third stage is characterized by the functional degeneration of the antheridium, which may be formed only when the ascogonium has completed the portion of the cycle in which fertilization would be possible and has already entered upon a stage of septation.

In the fourth group, as in *Aspergillus flavus*, *A. fumigatus* and *A. Fischeri* (Dangeard, 1907; Domaradsky, 1908), the antheridium is no longer formed. Only one helical ascogonium is formed which divides into binucleate cells and develops ascogenous hyphae in the usual way.

In a fifth group, as in *Penicilliopsis clavariaeformis*, as far as previous observations of the author extend, the formation of the fructification is no longer introduced by the formation of an ascogonium. Conidiophoric coremia radiate laterally or teminally without apparent reason (Fig. 115, 2, outer right) and change into perithecia in a still unknown manner.

Apparently there has taken place in the Aspergillaceae a gradual degeneration of sexuality, because of the retardation in the formation of the antheridium. The *Penicillium "crustaceum"* group is apparently still potent sexually; it may be directly connected to *Gymnoascus Reesii*. In other forms, as *P. Wortmanni*, the antheridium is formed when the ascogonium has already become multinucleate and hence may no longer be fertilized by the uninucleate antheridium. In still other forms, as in

the *A. herbariorum–repens* group, the antheridium is still more retarded and may only function when the ascogonium is already septate. Occasionally it may be entirely absent. In other forms, as *A. flavus* and *A. fumigatus*, the antheridium is entirely suppressed and the formation of fructifications proceeds only from the ascogonial helix. In a fourth stage, in *Penicilliopsis clavariaeformis*, the ascogonia are probably no longer formed and the development of the ascogenous hyphae takes place pseudogamously. These two important facts, that all these types occur so close together and that the different forms are often variable in behavior, allow one to conclude that the reduction of sexuality is still recent and has not yet become stabilized.

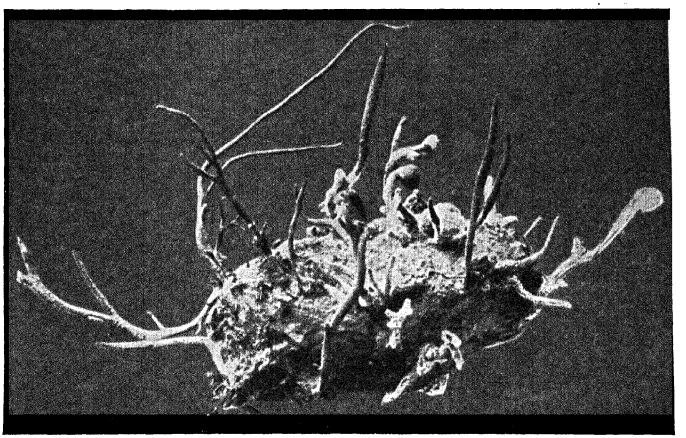


FIG. 115.—*Penicilliopsis clavariaeformis*. Left, coremia; right, young fundament of fructification; center, half-mature fructification. (Natural size.)

According to the further fate of the fructification fundaments in the Aspergillaceae group, two types may be distinguished. In the first type, to which belong the majority of the above forms, as *A. herbariorum*, *A. fumigatus*, *Penicillium Wortmanni* and *Scopulariopsis* sp. (*Acaulium albonigrescens*), the ascogenous hyphae divide without resting periods into binucleate cells which, on fusion of their nuclei, develop asci. They gradually dissolve the inner layers of the fructification parenchyma and providing nourishment for the maturing ascospores. At maturity the perithecia consist of a more or less solid pseudoparenchymatous sheath which is filled with a brownish spore powder and generally opens at the top by the decay of the cover. In *Aspergillus nidulans*, the fructifications do not arise free on the mycelial mat but are embedded in peculiar bladder-like sheaths (Fig. 116, 3). These are formed because the neighboring hyphae next the mycelial cover do not branch further, and the end cells

of the ultimate branches swell and thicken their membranes (Fig. 116, 5). To this first type also belongs *Penicilliopsis*, whose fructifications are divided into several ascigerous chambers by additional sterile veins differentiated from the ground tissue.

In the second type, which is only investigated in a representative of the *Penicillium Brefeldianum* group, the sterile ground tissue first goes through a resting period. About a week after its formation, it thickens its membrane and changes in a stony sclerotium. In its interior lie inconspicuous, aseptate, ascogenous hyphae, recognizable by their more refractive content.

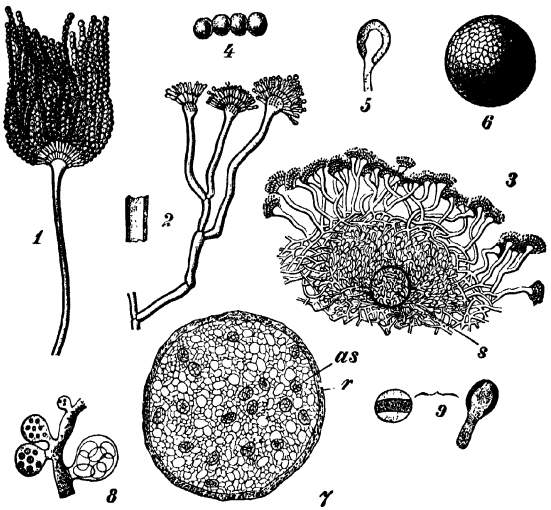


FIG. 116.—*Aspergillus nidulans*. 1, 2. Conidiophores with branched phialides. 3. Perithecium, *s*, surrounded by conidial mycelium. 4. Conidia. 5. Vesicle. 6. Perithecium. 7. Section of perithecium; *as*, ascus; *r*, rind. 8. Young asci. 9. Germinating ascospore. (1, 2 × 230; 3 × 120; 4 × 1,000; 5, 8 × 400; 6 × 85; 7 × 170; *after Eidam*, 1883.)

In this condition the sclerotia seem very like the sterile vegetative sclerotia of the other orders and, even in *Aspergillus* and *Penicillium* several species are known whose sclerotia are really sterile, forming only a resting condition of vegetative mycelia. Under favorable conditions, they develop directly to a mycelium. If, however, one sows the sclerotia of *Penicillium Brefeldianum* which has been carefully investigated by Brefeld, and by B. O. Dodge, one observes that only the aseptate ascogenous hyphae possess life while the sterile ground tissue is passive and gradually consumed by the ascogenous hyphae. About 7 to 8 weeks after the sowing of the perithecia, the ascogenous hyphae which extend from the center of the fructification (Fig. 117, *F*) are divided into short, cylindrical, apparently binucleate cells. Out of many of them

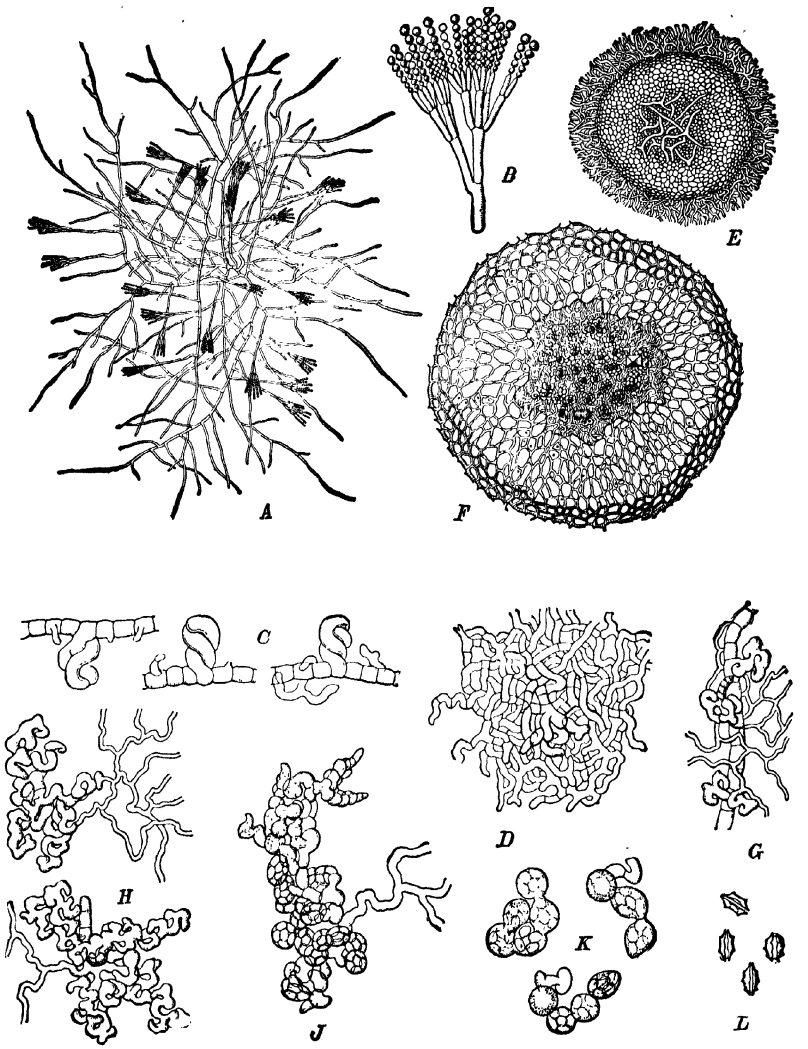


FIG. 117.—*Penicillium "crustaceum."* *A*. Mycelium with conidiophores. *B*. Single condiophore. *C*. Young copulation branches. *D*. Growth of ascogenous hyphae in the knot of peridial hyphae. *E*. Young perithecium before hardening of the walls. *F*. Sclerotic perithecium. *G* to *K*. Development of asci. *L*. Ascospores. (*A* × 60; *B* × 315; *C*, *D*, *G* to *J* × 630; *E*, *F* × 150; *L* × 800; *after Brefeld*, 1874.)

there grow thicker buds whose tips coil spirally (Fig. 117, *G*). On their curved outer surface there arises a branch which curves upward, coils and forms a new branch, etc., so that the different branches together form a serpiform main axis on whose convex sides there appear small branches (Fig. 117, *I*). The cells of the branches become spherical asci.

Besides these thick buds, thinner branches coiling like tendrils grow out of the ascogenous hyphae (Fig. 117, *G*). They elongate rapidly and penetrate the sterile ground tissue, thereby making room for the development of the asci. They seem to be nurse-hyphae and in this sense are analogous to the haustoria of the parasitic forms and the ooblastema filaments of the Florideae.

The animation of the sclerotia proceeds gradually from the center to the surface. Four to six weeks after germination, the first ascospores capable of germination are found in the sclerotia while the last asci still form mature spores 5 months later. The ascus walls gradually degenerate and the spores lie free inside the brown perithecial rind, which consists of two or three layers of periclinal cells. By rupture or decay of this rind, the ascospores are liberated. They possess a double membrane and a meridional furrow like most members of the Aspergillaceae (Fig. 117, *L*); the exospore is ruptured at germination and the endospore develops one or more germ tubes.

Onygenaceae.—This family has so far been found on animal substrates, hoofs, horns, hides, claws, feathers, teeth, etc., and in this sense forms a group sharply limited biologically. In the well-known *Onygena equina* the fructifications (Fig. 118, 1) are up to 1 cm. in height. They consist of solid homogeneous coremia which abjoint on their upper surfaces so many thick-walled hypnospores (Fig. 118, 2) that they seem to be covered by a brownish powder. Later they are differentiated into a solid stipe, composed of parallel hyphae, and a somewhat looser head, consisting of radiating hyphae. Around the latter, on its outer surface and toward the stipe, the hyphae intertwine to a firm pseudoparenchymatous peridium. Their connection with the central ground tissue, however, remains to maturity when they have become capillitium.

The processes which occur in spore formation have been too little investigated. In numerous places inside the head there are formed from the hyphae, two short septate branches which coil spirally into a solid knot and in an unknown manner give rise to the spores. In these relationships, they are superficially like *Penicillium*, but they have not been studied cytologically (Fig. 118, 3).

At maturity the cavity of the head is filled by a dark spore mass between which run the capillitium threads, generally starting at the base (Fig. 118, 4). The peridium is ruptured irregularly or around the base of the head and the spores scattered. They germinate directly after a resting period, which may be shortened by placing the spores in a mixture

of HCl and pepsin corresponding to the gastric juice. Immature ascospores and gemmae germinate without this stimulation (Ward, 1899; Brierley, 1917).

Trichocomaceae.—The Trichocomaceae are a poorly known family of the warmer regions. *Trichocoma paradoxa* (E. Fischer, 1890) grows on dead wood and forms fructifications up 1 cm. in diameter and 2 cm. high. Out of a woody-brown, patelliform, basal sheath, resting on the substrate, there arises a more or less columnar tissue. It consists of a system of faveolate tubular chambers which run up from the base of the fructification and are filled by the spore mass. The maturing of the fructification apparently takes place basipetally. The asci arise by a swelling of the binucleate members of the ascogenous hyphae. The development of this peculiar family is still entirely unknown.

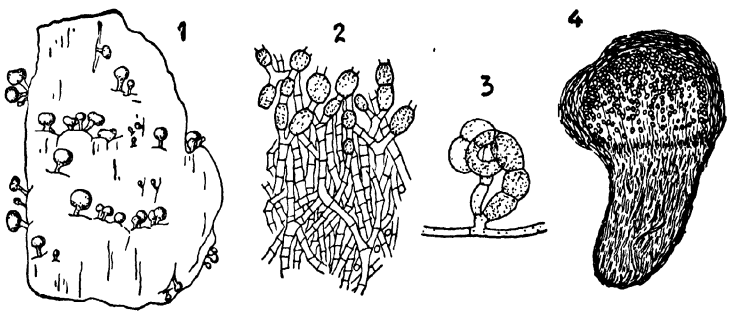


FIG. 118.—*Onygena equina*. 1. Fructifications on a piece of horn. 2. Section through the periphery of a young fructification. The terminal portions of the hyphae are forming gemmae. 3. Branches of a hypha whose cells will become asci. 4. Median section of an immature fructification. (1 × ⅔; *after Ward*, 1899.)

Terfeziaceae.—This and the following family are only known in the mature condition, and in the structure of their fructifications are next to *Penicilliopsis;* they are hypogaeous, however; furthermore, no conidia have been detected.

Terfezia Leonis is found in the Mediterranean region under *Cistus* and *Helianthemum* bushes with which they apparently form mycorrhizas. The fructifications reach the size of a fist and are divided by sterile veins into ascigerous portions which gradually run outward into a soft peridium. They are edible and appear in the markets in the near East as "Kames" and in North Africa as "Terfez." The Romans and Greeks also knew them.

Probably the Terfeziaceae do not belong to this order. As rapidly as the genera formerly placed in this family have been investigated cytologically and ontogenetically, they have been transferred to the Tuberales. So far *Terfezia*, the only remaining genus, has not been investigated.

Elaphomycetaceae.—This family may be divided into two tribes each with a single genus, the Elaphomyceteae and the Mesophellieae, the former widely distributed in Europe and America with many species confined to Italy, the latter confined to Australia.

The fructification in *Elaphomyces cervinus* (*E. granulatus*) and *E. muricatus* develops from a complex hyphal knot which is first differentiated into an outer layer, the fundament of the crust and cortex, then the inner layer is separated into peridium and core. The peridium becomes more or less pseudoparenchymatous traversed by aeriferous

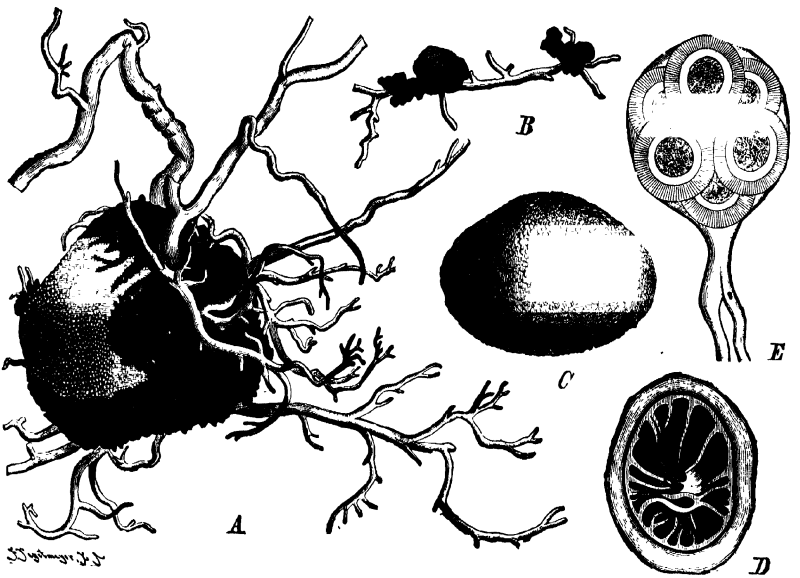


FIG. 119.—*Elaphomyces cervinus*. *A*, *B*. Mature fructifications attached to pine roots. *C*. Mature fructification. *D*. Section of nearly mature fructification. *E*. Ascus. (*A* × 1½; *C* natural size; *after Reess and Fisch*, 1887.)

veins, while the core remains a loose hyphal tissue. The sexual processes have not been observed, but the ascogenous hyphae grow out from the inner wall of the peridium into the core and by repeated branching form groups of asci, (Fig. 119, *E*) which early disappear. In some species these spore masses form small balls resembling those of *Polysaccum*, while in others they completely fill the central cavity (Reess and Fisch, 1887).

The ontogeny of the fructifications of the Mesophellieae have not yet been studied, but observations on the morphology of the mature fructifications suggest that it may be similar to that of the Elaphomyceteae. In *Mesophellia castanea* the sexual organs appear in little loculi near the aeriferous veins of the peridium. Two large septate

hyphae grow side by side, and coil once or twice. The terminal cells elongate and fuse near their tips. Ascogenous hyphae grow from the basal cell of one of these hyphae, suggesting that there is a differentiation into trichogyne and ascognonium, although the nuclear history could not be followed in the material available. The ascogenous hyphae produce asci in most of their cells, as in the Onygenaceae and Trichocomaceae (C. W. Dodge, 1929).

In *M. castanea*, the hard central core has comparatively few trabeculae connecting it to the peridium which at maturity consists of a single layer, suggesting the peridium of *Elaphomyces muricatus* in its mottled appearance. In *M. sabulosa*, the peridium is cut off from the gleba by a well marked zone of fission and quickly gelifies so that at maturity it consists largely of a shell of sand held together by a gel. In *M. arenaria*, the rind is differentiated into a peridium and cortex having the texture of strawboard as seen in section.

Elaphomyces forms mycorrhizas with the roots of conifers, (Fig. 119, *A–B*) especially *E. muricatus*, *E. variegatus* and *E. cervinus*. The latter has been used since the Middle Ages as an aphrodisiac in folk medicine. All three species are often infected with *Cordyceps ophioglossoides* and *C. capitata* of the Hypocreales.

Summary.—The Plectascales hold an important position in the Ascomycetes as below they have their morphological relations with the Endomycetales and Zygomycetes, and have the beginnings of a varied upward development. Their imperfect forms, conidia, are basically the same as in these groups, but they have developed in three directions. One is represented by the Aspergillaceae; morphologically it inclines toward the *Syncephalastrum–Syncephalis* group and in this sense forms a branch of the *Choanephora–Piptocephalis* series. While in *Mucor*, *Sporodinia*, etc., spore formation is still normally endogenous, in *Choanephora*, with liberal food, it is retarded and becomes exogenous, and in *Syncephalastrum* and *Syncephalis* it is fixed in an exclusively exogenous type. The *Aspergillus* group has proceeded a step beyond the *Syncephalis* type, however, and on its sporangia forms purely exogenous conidia. Just as in the further development of the *Syncephalis* type, the sporangia which have become functionless collapse into gibbous basal cells (as in *Piptocephalis*); in the *Aspergillus* group the sporangia degenerate and through a series of intermediate forms the *Penicillium* type is reached, where long spore chains on flask-shaped phialides are cut off at the top of undifferentiated conidiophores.

The second direction is represented by *Thielavia*. Its origin is still unknown; its morphological significance lies in endogenous conidial formation by the splitting of the conidial membrane. The third direction is represented by *Ctenomyces*. Here for the first time the condiophores intertwine into special pycnia with lysigenous cavities.

Like the imperfect forms, the sexual organs are directly connected to the Endomycetales and Zygomycetes, only the dynamic differentiation between the male and female copulation branches becomes morphological and, in the majority of forms, has led to special antheridia and ascogonia which are characteristic both in form and function. As the imperfect form, so the sexual organs show development in three directions. A first direction (*Monascus–Magnusia*) is distinguished by the functional development of the female copulation branch. This no longer participates as a whole in fertilization but is differentiated into a trichogyne and a female gametangium, the ascogonium. Herein lies the root of the relationships in many higher Ascomycetes.

A second series (*Gymnoascus–Aspergillus–Penicillium* group) develops in the reverse direction, with the gradual disappearance of sexuality. Already in the simpler forms the sexual act has become facultative. In the higher forms, the formation of the antheridium is more and more delayed and can only function when the ascogonium has already passed the stage of maturity for fertilization and has become multinucleate or is already septate. Hence the ascogonia probably develop parthenogenetically. When the antheridia are still formed, perhaps they only fulfil a physiological function of nourishment, and hence are called "trophogones" by Dangeard (1907). They are soon no longer formed and the ascogonia develop alone.

In the third series (*Penicilliopsis–Elaphomycetaceae*) the sexual organs no longer initiate the formation of fructifications but function within them.

While the imperfect forms and sexual organs of the Plectascales correspond with the Endomycetales and Zygomycetes in the further development of the zygotes, there appears a new factor, the dicaryophase and the development of the ascogonial cells to ascogenous hyphae. Thereby the developmental scheme of the Plectascales is lengthened by one member from that of the Endomycetales (p. 146):

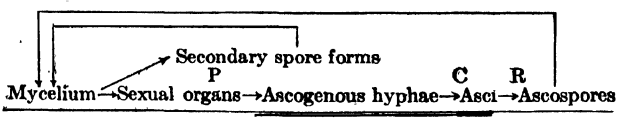


DIAGRAM XIX.

In several forms the ascogenous hyphae show a peculiar separation into two phases; thus in *Aphanoascus* they first grow spirally ("primary" ascogenous hyphae), the branches again coil ("secondary" ascogenous hyphae); only the second generation forms the asci. More sharply distinct is the division in *Penicillium Brefeldianum* where the ascogenous hyphae are developed into a resting and a spore-forming period. At present no interpretation of this change of ascogenous hyphae is evident; we meet it, however, in the Erysiphaceae.

Along with this development of the ascogenous hyphae, there takes place in the Plectascales a gradual development of fructification which in the highest hypogaeous forms rises to the level of *Glaziella*, Tuberales and Hysterangiaceae.

If one attempts to divide the Plectascales from this point of view, one arrives at a scheme such as is represented below. It is obvious that the groups in this scheme may be disproportionately evaluated. Thus from *Amauroascus*, through *Gymnoascus*, *Aphanoascus* and *Aspergillus*, there is a gradual transition toward *Penicillium*, while on the other hand, *Thielavia* and *Monascus* form sharply defined types and hence are often regarded as representatives of separate families. Similarly the four highest families of the Plectascales may be regarded as natural.

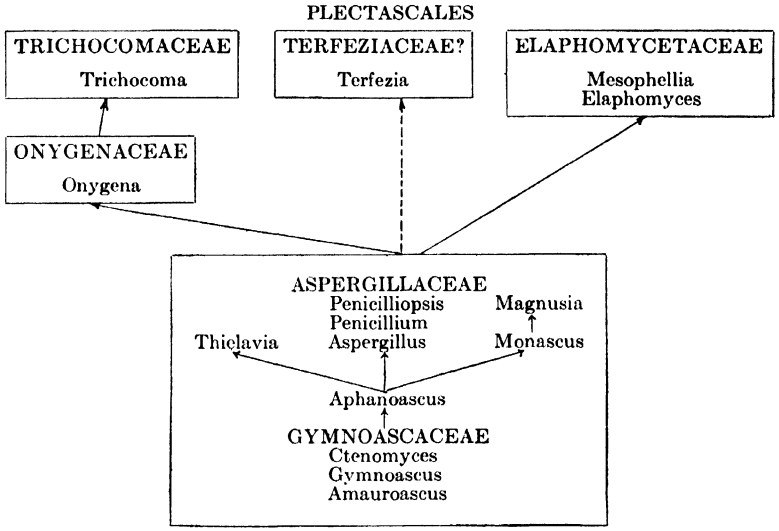


DIAGRAM XX.

As may be observed in the scheme at the close of the book (p. 618), there may be derived not less than five orders entirely or partly hypothetically from Plectascales-like types, of which the present known genera form only a small remainder. If one imagines the ascogenous hyphae short, so that the asci are joined into a tuft, one obtains the Perisporiales from the *Thielavia*-like forms. If one imagines that at maturity the perithecium is opened by an ostiole, one proceeds from the simpler Gymnoascaceae and Aspergillaceae to the simpler saprophytic Hypocreales and Sphaeriales. If one imagines that the mycelial mat develops stromatically in the *Gymnoascus* and *Aphanoascus*-like forms, and that the hyphal covers are intertwined to a plectenchyma not only around the sexual organs, but throughout the whole extent, one comes to the Myriangiales and Pezizales.

CHAPTER XIV

PERISPORIALES

The Perisporiales differ from the Plectascales in that their asci are not irregularly formed in the interior of the perithecia but in a fascicle (or umbel), free at maturity, attached at the base and generally still without paraphyses; thus the asci all stand at the same height. Externally, many Perisporiales may not be distinguished from the Aspergillaceae (*e.g.*, *Thielavia* group) and only an investigation of the manner of formation and arrangement of the asci offers a solution of the systematic position of the fungi in question.

In contrast to the Plectascales, the Perisporiales are obligate parasites in which the perithecia, generally still cleistocarpous, as in the parasitic Plectascales, are extramatrical, in a position to take an active part in dissemination. Biologically they form a peculiar developmental series from the endoparasitic to the ectoparasitic method of life, whose end forms are distinguished by a special asterinoid habit (Arnaud, 1918); this type includes ectoparasitic forms, chiefly in damp climates, which spread radially over the surface of the host by aerial mycelia and derive their nourishment by the formation of haustoria or sinkers.

In this sense the Perisporiales are circumscribed, half morphologically, half biologically. They form a transitional order from the Plectascales to the Pyrenomycetes and hence to a high degree their limits are determined by the subjective measurements of individual investigators. In the following discussion, we will recognize three families: the Erysiphaceae, the Perisporiaceae and the Englerulaceae. The Erysiphaceae include the forms with white aerial mycelium; they are cosmopolitan but are best developed in the temperate zone. In addition to their hyaline extramatrical mycelium, they are distinguished by the development of imperfect forms and by their unicellular ascospores. The Perisporiaceae and Englerulaceae include those forms with more or less dark-colored aerial mycelium. They are mostly tropical and subtropical. Imperfect forms have been found with certainty only in a single genus. Their ascospores are generally septate. The Englerulaceae differ from the Perisporiaceae by a peculiar histolysis of their perithecial wall, whereby their mature fructifications attain a half-open Discomycetous structure.

Erysiphaceae.—The powdery mildews show most markedly the character of the Perisporiales. They form a very homogeneous, sharply defined group and are parasitic on Angiosperms. Together with the

rusts they belong to the few groups of obligate parasites which up to the present have resisted all attempts at culture on artificial substrates; as in the rusts, they do not kill the affected host tissue but may stimulate it to slight hypertrophies.

The hyphae are strongly septate; their cells are uninucleate; the haustoria alone are sometimes multinucleate. Their walls are hyaline, except in *Sphaerotheca mors-uvae* where they become dark in age.

As regards their behavior toward the host, they may be arranged in a noteworthy series from endoparasitic, through hemiendophytic, to ectoparasitic forms. Their lowest endoparasitic stage is represented by

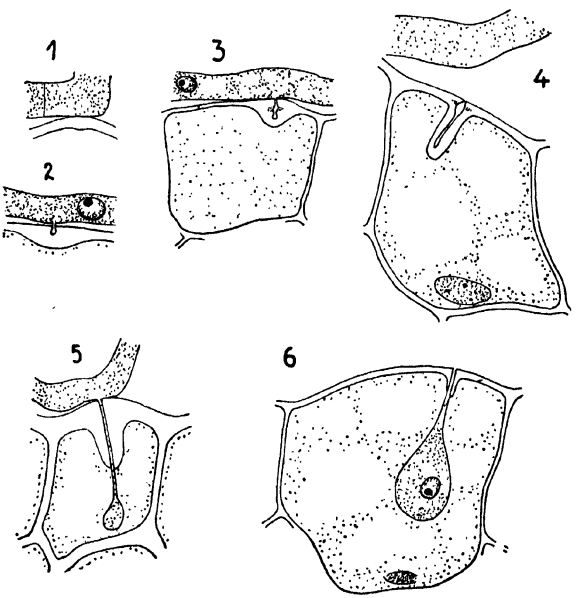


FIG. 120.—*Erysiphe Polygoni* on *Geranium maculatum*. Development of haustoria. (× 1,200; *after G. Smith*, 1900.)

Leveillula taurica (*Oidiopsis taurica*). In it the mycelium lies, as in many parasites, in the intercellular spaces of the host leaves; only in the later stages of conidial formation do the hyphae emerge on the surface of the leaf and then form, like the other Erysiphaceae, an arachnoid or felty mat. These extramatrical hyphae cling by appressoria to the surface of the leaf; on this surface, however, they form no haustoria but nourish themselves, as do the hemiendophytic forms, by branches which penetrate the interior of the leaf through the stomata.

In the hemiendophytic stage, as in *Phyllactinia*, the mycelium lives in the manner characteristic of mildews, extramatrically on the

surface of the leaves. This external mycelium does not penetrate the epidermal cells by haustoria, but puts forth special branches of limited length through the stomata into the mesophyll (Fig. 121, 2) where they secure nourishment.

The ectoparasitic stage includes all the other Erysiphaceae. These are entirely extramatrical and form a loose white covering on the surface of the host, so that it seems dusted with flour. The hyphae creep about the epidermis and from time to time form short branches. Where these come into contact with the wall of the epidermis, they spread out into a simple or lobate appressorium. The epidermal wall begins to swell and stains deeply (Fig. 120, 1). The very slender hyphal tip bores through

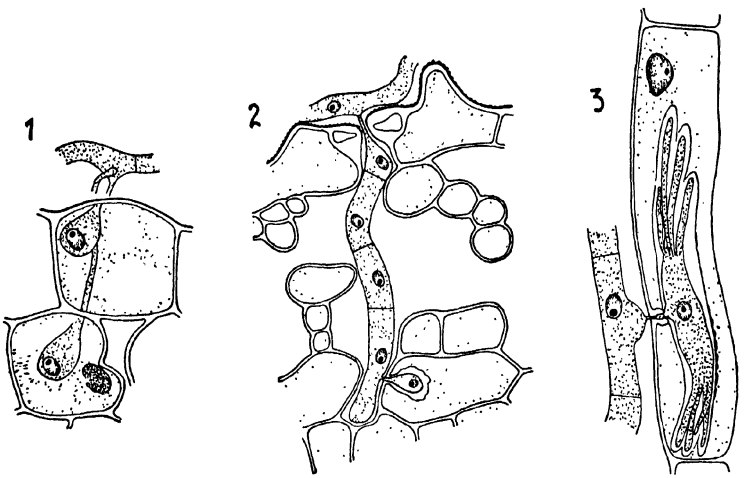


FIG. 121.—1. *Uncinula Salicis* on *Salix discolor*. Haustoria which have penetrated the hypodermal cell layers. 2. *Phyllactinia corylea* on *Cornus stolonifera*. Hyphal branch penetrating the mesophyll. 3. *Erysiphe graminis* on *Poa pratensis*. Haustoria. (1, 2 × 600; 3 × 1,200; *after G. Smith*, 1900.)

the cuticle and the cell wall into the interior of the epidermal cell (Fig. 120, 2 to 4) and expands there into a saccate haustorium (Fig. 120, 5 and 6). This simple tuberiform or saccate knot is the usual type of haustorium in this group. Only in *Erysiphe graminis*, the haustoria grow laterally to long filiform lobes (Fig. 121, 3). Generally the haustoria remain limited to the epidermal cells; only in *Uncinula Salicis* they may penetrate to the subepidermal cells but never further (Fig. 121, 1).

In spite of this extreme ectophytism which only differs from pure epiphytism in the formation of haustoria, and in spite of their hyaline walls, the Erysiphaceae are very resistent to external influences; *e.g.*, they can thrive on parts of plants which are in full sunlight the whole day. They are found from the polar regions to the tropics but

prefer damp climates. The only endophytic species, *Leveillula taurica*, belongs to dry subtropical regions whose phanerogams are generally xerophytes with a very thick epidermis. Further it appears that the Erysiphaceae in the tropics generally only propagate by imperfect forms and that the perithecia degenerate.

They are also sharply specialized even in their ectophytism (Salmon, 1900, 1903; Steiner, 1908; Blumer, 1922; etc.). From the numerous forms so far studied, except for *Erysiphe cichoracearum*, none is able to go beyond a single host genus, and is often limited to a single species

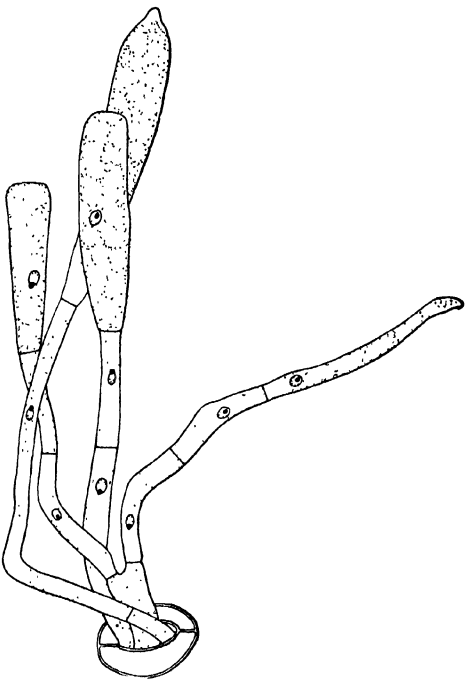


FIG. 122.—*Leveillula taurica*. Conidiophores. (× 830; *after Foëx*, 1913.)

or group of species within the genus. Salmon (1904, 1905) has shown, however, that here our observations on the fundamental relationships need clarification. If one wounds old leaves whose cuticle normally resist infection (*e.g.*, if one cuts away a piece of epidermis), the fungus may then infect the mesophyll. In this manner, transitions between various biological strains might be possible.

As imperfect forms, only conidiophores and conidia are known; earlier pycnia were ascribed to the Erysiphaceae but they have since been demonstrated to be the fructifications of a parasitic imperfect, *Cicinnobolus Cesatii*. The conidiophores are at first formed on both sides

of the leaf, but later, in proportion as perithecia are formed on the upper side of the leaf, they become limited to the lower side. According to the manner of cutting off the spores, they are divided into two types; in the first type, which includes the endo- and hemiendophytic forms, the

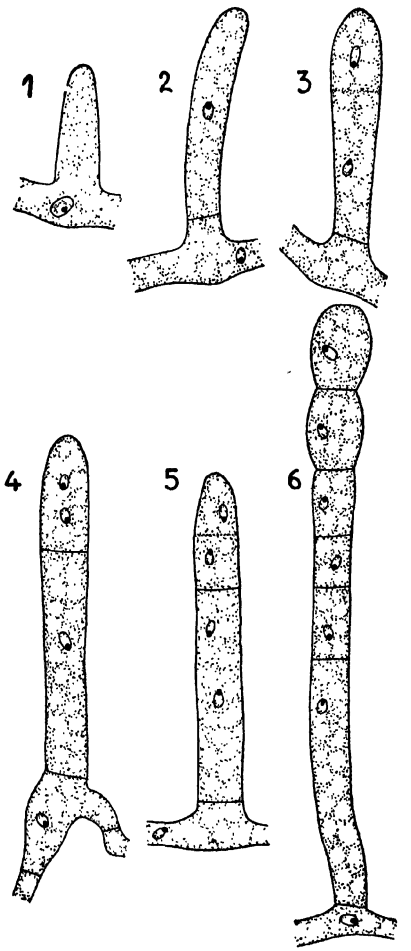


FIG. 123.—*Sphaerotheca Humuli.* Development of conidiophore. (× 830; *after Foëx*, 1913.)

conidia are cut off singly, in the ectoparasitic forms they arise in chains (Foëx, 1912, 1913; Bezsonov, 1913).

In the first type, *Leveillula taurica* (Fig. 122), the hyphae collect in the substomatal cavity to dense, almost pseudoparenchymatous knots, whence radiate the mostly unbranched, aerial hyphae (conidiophores)

whose upper cells form conidia. When this falls off, the subterminal cell (or conidial mother cell) divides again into two daughter cells, the upper of which develops to a new conidium. The development of *Phyllactinia* proceeds similarly, except the conidiophores are formed only on the superficial mycelium.

In the second type, *e.g.*, *Sphaerotheca Humuli* (*S. Castagnei*) a protrusion forms on a hypha above a nucleus (Fig. 123, 1); this elongates and divides into two cells of which one remains connected with the sporiferous hypha while the other projects over it (Fig. 123, 2). The latter is the mother cell of all future conidia; it cuts off successively a series of daughter cells which round off to conidia, or first divided into two and the resulting daughter cells change to conidia (Fig. 123, 3 to 6). Thus the mother cells in this group, which includes *Erysiphe graminis*, *E. cichoracearum*, *Sphaerothecca pannosa* and *S. mors-uvae*, lie directly on the sporiferous hypha. In another group, as *Erysiphe Polygoni* and *Uncinula Salicis*, it is separated from the sporiferous hyphae by a longer or shorter stipe cell.

The conidia are hyaline, uninucleate and generally only capable of germination for a short time. As they are formed in enormous numbers, they facilitate a very rapid dissemination. In damp air or water, they develop one or more germ tubes on their narrow side.

As they often appear months before the perithecia and as on many hosts the perithecia are unknown, many Erysiphaceae have been described as imperfects; thus the conidial forms of *Leveillula taurica* type were placed in the imperfect genus *Oidiopsis*, the conidial forms of the *Phyllactinia* type were in *Ovulariopsis* and the conidial forms of the ectophytic type in *Oidium*. Occasionally (although the expression has nothing to do with oidial formation) this designation is still used in plant pathology.

The perithecia generally begin to appear in the course of the summer. From two neighboring hyphae there arises a thick, slightly ovoid ascogonium and a slender, somewhat curved antheridium; often they coil about each other. Like the hyphal cells, they are both originally uninucleate, and separated from the sporiferous hypha by a septum. The male nucleus divides, and a basal stipe cell is cut off from the apical antheridium (Figs. 124, 2; 126, 1 and 2), exceptionally the ascogonium may also undergo a division.

The further development of both copulation branches has been the object of considerable controversy. In a first group, as in *Erysiphe Polygoni* (*E. communis*) on *Trifolium* and *Mellilotus* (Harper, 1896), in *Sphaerotheca Humuli* on *Humulus* (Harper, 1895; Blackman and Fraser, 1905, denied by Dangeard, 1907), in *Phyllactinia corylea* on *Fraxinus americana*, *Corylus americana*, *Celastrus scandens* and *Betula lutea* (Harper, 1905) and in *Sphaerotheca mors-uvae* on *Ribes* sp. (Bezsonov,

1914), the antheridium comes into open connection with the ascogonium and the male nucleus migrates into the ascogonium and fuses with the female (Figs. 123, 3; 126, 3). In *S. mors-uvae*, it goes through another division before migration, so that one daughter nucleus migrates into the

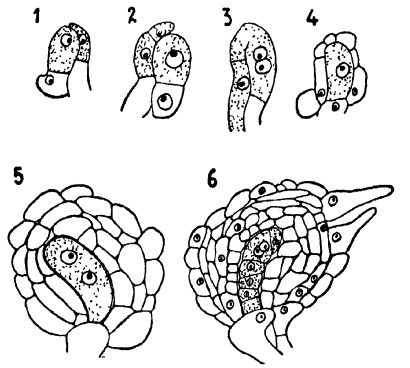


FIG. 124.—*Sphaerotheca Humuli*. Development of perithecia. 1. Young antheridium and ascogonium. 2. The antheridium divided into antheridial cell and stalk cell. 3. Plasmogamy. 4 to 6. Development of fertilized ascogonium. (× 500; *after Harper*, 1896.)

ascogonium while the other remains behind in the antheridium and degenerates. In a second group, as in *Erysiphe Polygoni* (*E. Martii*) on *Pisum sativum* and *Ranunculus acris*, *E. cichoracearum* on *Sonchus oleraceus*, *Phyllactinia corylea* on *Corylus Avellana*, in *Uncinula Salicis* on

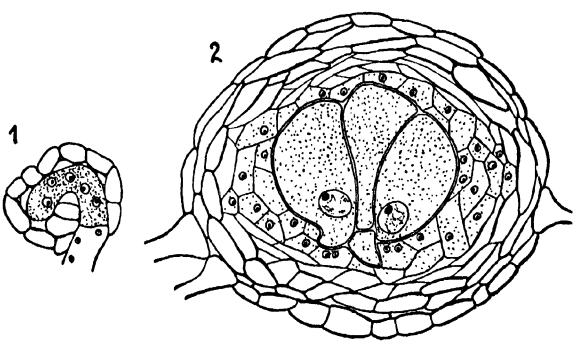


FIG. 125.—*Erysiphe Polygoni*. 1. Primary ascogenous hypha with five nuclei. 2. Longitudinal section through a young perithecium with three asci; the perithecial wall is already differentiated. (× 470; *after Harper*, 1896.)

Populus (all according to Dangeard, 1907) and in *Sphaerotheca Humuli* var. *fuliginea* on *Melampyrum* (Winge, 1911), fertilization is absent and the male nucleus degenerates in the antheridium. Thus in the Erysiphaceae the relationships are apparently the same as in the Plectascales. Although the sexual organs are normal morphologically, sexual-

ity is degenerating; in some species the sexual act still occurs, in others it is absent and the ascogonia develop parthenogenetically; in still others, as in *Sphaerotheca Humuli*, the behavior varies according to circumstances

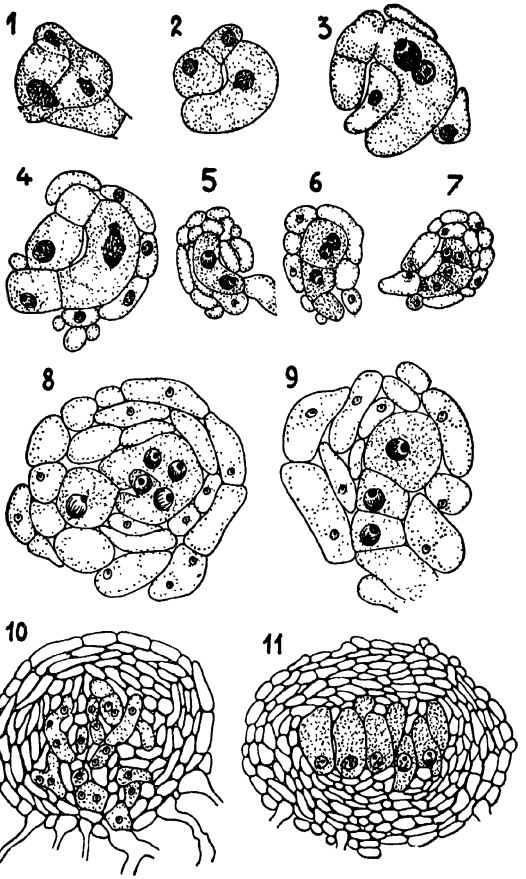


FIG. 126.—*Phyllactinia corylea*. 1. Coiled copulation branches. The male nucleus has divided to form a stalk cell and antheridial cell. 2. Antheridium completely divided into stalk cell and antheridial cell. 3. Plasmogamy. 4. Caryogamy. 5. Outgrowth of primary ascogenous hyphae. 6, 7. The binucleate penultimate cell of the primary ascogenous hypha (the ultimate cell is in the next section). 8, 9. The penultimate cell develops secondary ascogenous hyphae. (These figures represent successive, serial sections of the same hypha.) 10, 11. Young fructifications, the former showing ascogenous hyphae, the second young asci. (1 to 4, 8, 9 × 670; 5, 6 × 250; 4, 7, 10 × 330; 11 × 200; *after Harper*, 1905.)

and the ascogonia may continue their development with or without fertilization.

According to the type of the further development, the fertilized or the unfertilized ascogonium grows while the antheridium collapses to a

thick hypha which in *P. corylea*, and in the forms of *Erysiphe Polygoni* (*E. communis*) on *Ranunculus acris* investigated by Dangeard includes, in a manner still unexplained, several bi- and several uninucleate cells; in the form of *E. Polygoni* on Leguminosae investigated by Harper, septation is first absent apparently because of very rapid elongation (Fig. 125,1), so that the hyphae have five to eight nuclei and only subsequently divide into single cells; thereby the subterminal cell is binucleate (Fig. 126, 6 and 7). The relationships are difficult to follow cytologically, as the copulation branches are already surrounded by a thick hyphal knot into which the primary ascogenous hyphae, growing out from the ascogonium, penetrate with irregular twistings. In a manner still to be studied, one or more of the binucleate cells grow out of this primary ascogenous hypha to secondary ascogenous hyphae (Fig. 126, 8 and 9) which branch many times, and change the terminal cells to asci with nuclear fusion.

In *Sphaerotheca*, alone of all the forms so far studied, the primary ascogenous hypha, itself growing from the ascogonium, proceeds directly to the formation of a single ascus. Thus, as in *Erysiphe Polygoni* the ascogonium develops to a multinucleate tube which divides simultaneously into several uninucleate cells and a subterminal binucleate cell (Fig. 124, 6). This subterminal cell develops directly to an ascus, with the fusion of its dicaryon. While each of the perithecia in the first type includes several (up to 20) asci, in the *Sphaerotheca* type it contains only one. In both, the primary ascus nucleus undergoes three steps in division, whereupon the daughter nuclei cut out of the protoplasm eight (or, on account of abortion, only four or two) unicellular, later brown ascospores. These, probably the largest unicellular spores in the fungi, in *Phyllactinia corylea* attain a length of over 50 μ. They are liberated by irregular rupture or by crumbling of the peridium.

An interpretation of the relationships of the first and second types of development seems to be possible only on the basis of relationships described in the Plectascales. The first type (*Phyllactinia–Erysiphe*) may be directly referred to the *Aphanoascus–Penicillium* type, in which the ascogenous hyphae divide into two phases of which only the second is sporogenous. Only in the *Phyllactinia–Erysiphe* type, and this seems to be a new character for the group, the first phase undergoes a gradual degeneration, while in *Phyllactinia corylea* and in *Erysiphe Polygoni* (*E. Martii*), as in the Plectascales, several binucleate cells are formed in the first phase so that several ascogenous hyphae result. There is only one binucleate cell in the form of *Erysiphe Polygoni* (*E. communis*) studied by Harper, consequently the number of ascogenous hyphae is limited to a single one which, by branching considerably, gives rise to a few asci.

This limited elongation in the first phase of the ascogenous hyphae may undoubtedly be called the new characteristic point of the Erysipha-

ceae (and of the Perisporiales altogether); for only by this limitation does there result that tufted arrangement of asci which forms the characteristic feature of the Perisporiales.

This degeneration goes still further in the *Sphaerotheca* type, for here the development of the subterminal cell to a secondary ascogenous hypha is also suppressed and the subterminal cell itself develops directly to an ascus.

If the interpretation is correct, the Erysiphaceae may be regarded as a branch of the Plectascales in which the first and then the second phase of development of the ascogenous hypha gradually disappears reaching an end stage in *Sphaerotheca*. It is, however, not permissible (as repeatedly occurs in the literature) to contrast the subterminal formation of asci in *Sphaerotheca* and their terminal formation in *Erysiphe* and *Phyllactinia* and to find fault with one or the other observation; for the sporogenous ascogenous hypha belongs in the two groups to different stages of development.

The second problem which arises in the consideration of the life cycle of the Erysiphaceae, is double fertilization. If the interpretation which Harper and others have given to their observations were correct, a first caryogamy occurs in the ascogonium and a second in the ascus. As was briefly discussed in the introduction to the Ascomycetes, it is at present impossible to clear up controversy over this point. As occasionally observations on material from different hosts have been combined, a source of error might lie here, as similar misinterpretations, resulting from mixing material of different biological strains, have occurred also in the Ustilaginales. In this case, one must assume that in the Erysiphaceae (as in the Agaricales of the *Hygrophorus conicus* type in the Basidiomycetes) the place of caryogamy varies, in one form, in the ascus, in the other in the ascogonium, and that, by a combination of these types, there is a deceptive picture of double fertilization.

At maturity, the perithecia agree in the essential characters of their structure with those of the Plectascales. They consist of a homogeneous, brown, hard, brittle rind consisting of plates, regular polygonal cells and of a hyaline nurse tissue in which the asci are imbedded (Hein 1927). This collective tissue within the brown rind, together with the asci, is occasionally referred to in systematic literature as "nucleus," centrum, kernel or core. In contrast to the Plectascales, the perithecia in the Erysiphaceae have assumed a protective function by wintering over, as well as the task of propagation. Perhaps the limitation of the number of asci to one and consequent reduction of the dimensions of the perithecia is connected with this new function and hence in the Erysiphaceae there appear problems similar to those which we have met in the Oomycetes.

This propagative function of the perithecia is facilitated by two important facts, by the development of special appendages and, in some forms,

by the special structure of the perithecial rind. Before the rind has completed its peridial structure, some of its cells develop to long appendages; these are generally characteristic and offer one of the most convenient points for the separation of genera. In *Erysiphe, Leveillula* (Fig. 127) and *Sphaerotheca,* they are simple, hyphal-like and intertwined with the mycelium; in *Podosphaera* (Fig. 128, 4) and *Microsphaera* (Fig. 128, 1 to 3), they are repeatedly dichotomously branched at the tips; in *Uncinula* (Fig. 128, 5 to 7), they are coiled more or less spirally at the tips; in *Typhulochaeta,* they are clavate and arranged in a ring consisting of

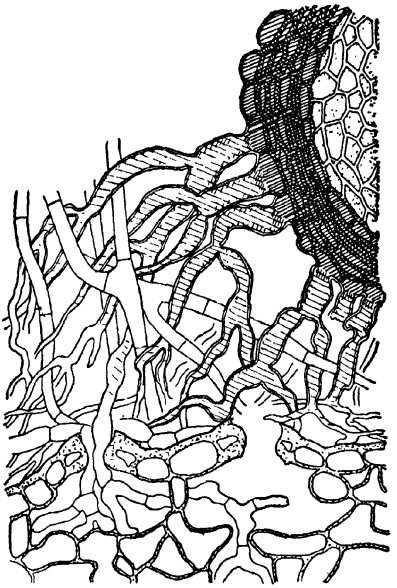


FIG. 127.—*Leveillula taurica.* Section through the lower surface of a leaf and the peridium of a perithecium, showing extra- and intramatrical mycelium and the hyphal appendages. (× 400; *after Arnaud,* 1921.)

two or three rows around the top of the perithecium; and in *Phyllactinia,* unbranched, but setiform and rigid, with a saccate base (Fig. 129, 1).

As regards the structure of perithecial wall, there are two groups. In *Sphaerotheca, Erysiphe* (Fig. 125, 2) and *Leveillula,* the rind (as in the Plectascales) is spread approximately evenly over the whole fructification; in *Microsphaera* and *Uncinula,* it possesses a dorsiventral structure consisting generally at the base of wide-lumened, thin-walled cells and at the top of narrow-lumened, thick-walled cells. Neger (1901, 1902) attempts to interpret these observations biologically as follows: in the first group, with the peridium symmetrical on all sides, the perithecia are generally sessile. Their appendages are interwoven with mycelium and

do not loosen even toward spring; if in the course of the winter, the perithecia dry, they shrink evenly so that the spherical form is not altered. The perithecia remain clinging to the substrate and only later, together with the mycelium, are washed away. Thus the appendages here serve for gripping the mycelium and indirectly, the substrate.

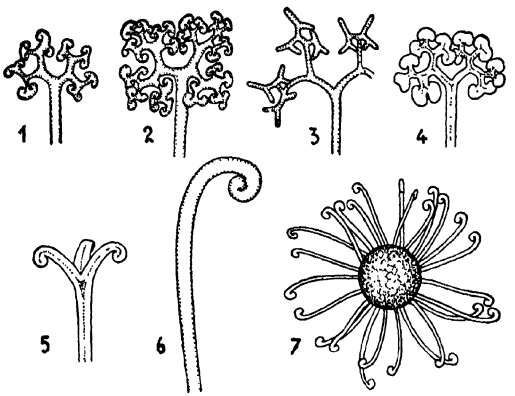


FIG. 128.—Types of appendages. *Microsphaera Alni*. 1. On *Syringa*. 2. On *Cornus alternifolia*. 3. Var. *Lonicerae*. 4. *Podosphaera Oxyacanthae*. 5. *Uncinula Aceris*. 6, 7. *Uncinula Sengokui*. (× 270; *after Salmon*, 1900.)

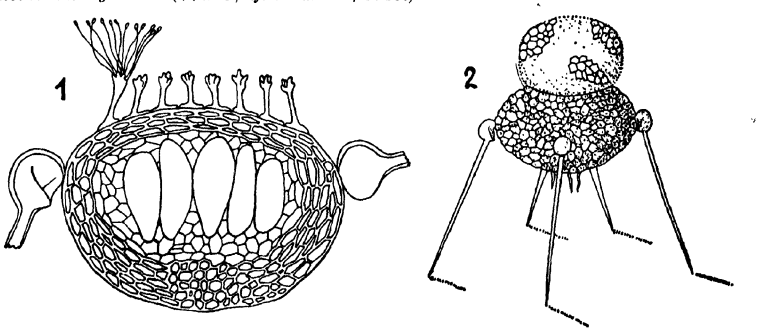


FIG. 129.—*Phyllactinia corylea*. 1. Perithecium with penicillate cells above, a turgid spherical cell on the right, a collapsed spherical cell on the left. 2. Erect perithecium with an apical drop of gel. (1 × 200; 2 × 100; *after Neger*, 1901.)

In the second group, with dorsiventral rind, the perithecia are mobile; they gradually break loose from the substrate, fall off more or less spontaneously and are carried away by external agents. This active loosening from the substrate is caused either by the action of the rind or of the appendages.

The coöperation of the rind in the liberation of the perithecia is credible for *Uncinula* and *Microsphaera*. Upon drying, the whole rind does not shrink evenly, but only its thin-walled, lower surface; this becomes more or less concave inwards and thereby (especially with

repeated drying and wetting) tears the hyphae with which it was attached to the substrate. Apparently, in these two genera, the appendages serve for passive dissemination; possibly they also favor clinging to a new substrate, as in some species of *Uncinula* they are also sticky.

The coöperation of the appendages in the liberation of the perithecia has only been demonstrated in *Phyllactinia*. The sac at the base of the appendage is thick walled on the upper side and thin walled on the lower side (Fig. 129, 1). In drought, the lower side wrinkles and bends down like a joint, thereby the perithecium is raised from the surrounding mycelium as upon stilts (Fig. 129, 2). Experiments in a desiccator have shown that the force developed is comparatively large: Four perithecia easily raise a cover glass of medium thickness. The clinging of the perithecia to the new substrate is not accomplished in *Phyllactinia* by the appendages but by peculiar tufts of hyphae at the top of the perithecia which swell to a hygroscopic, foamy drop of slime (Fig. 129, 2) and apparently, upon drying, attach the perithecia firmly.

A review of the more important genera here discussed (taken in part from Arnaud, 1921) is presented in the following scheme:

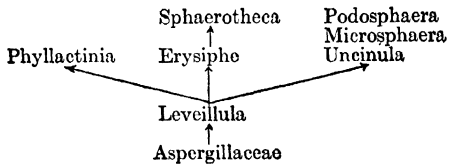


DIAGRAM XXI.

The polyascous *Leveillula–Erysiphe* group is regarded as primitive and the monascous *Sphaerotheca–Podosphaera* group, as derived. With this development, a decrease of intramatrical and increase of extramatrical mycelium occurs, *i.e.*, a transition from endoparasitism to ectoparasitism, and a consequent increase in the ability of the conidiophores to form spores. The *Erysiphe–Sphaerotheca* series is distinguished by undifferentiated, the *Uncinula–Podosphaera* series by characteristic appendages.

Several representatives of these genera cause plant disease, as *Erysiphe graminis* on cereals, *Uncinula necator* (*Oidium Tuckeri*) on grapes, *Sphaerotheca mors-uvae* on gooseberries, *S. pannosa* on roses, *S. Humuli* on hops, cucumbers, etc., *Podosphaera leucotricha* on apples and *Microsphaera alphitoides* (*Oidium quercinum*) on oaks.

Perisporiaceae.—In contrast to the Erysiphaceae, this family lacks sharp limits. It begins with forms with Perisporial characters, develops toward the Sphaeriales type and merges into this order in the Amphisphaericaceae and its relatives. This will be briefly discussed in four genera, *Lanomyces, Balladyna, Meliola* and *Parodiopsis.*

In *Lanomyces tjibodensis* (Gäumann, 1922c), parasitic on the leaves of *Castanopsis argentea* in the mountain forests of West Java, the hyphae are generally 2 to 3 nucleate; as those of *Leveillula taurica* they are pri-

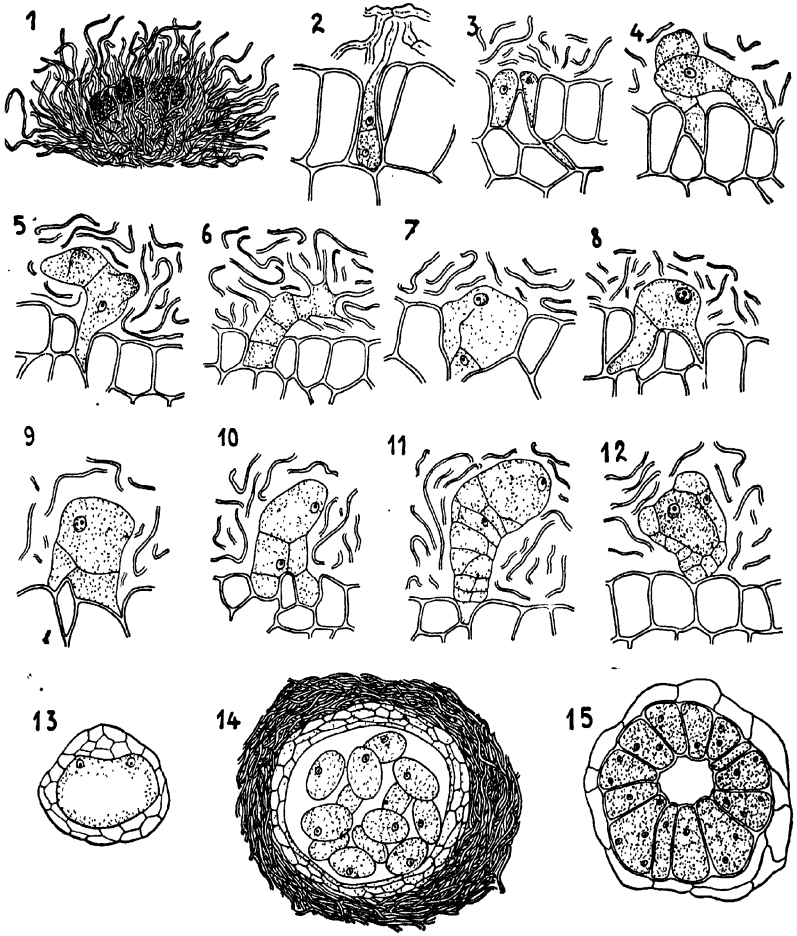


FIG. 130.—*Lanomyces tjibodensis*. 1. Extramatrical mycelium with three loosened perithecia. 2. Sinker penetrating between epidermal cells. 3, 4. Young copulation branches. 5, 6. Copulation branches which failed to mate and have hypertrophied. 7, 8. Fertilization. 9 to 13. Development of the young perithecium. 14. Section through a perithecium, showing both peridial layers. 15. Section through an immature perithecium; the outer peridial layer is left off, the ascospores are compressed. (1 × 55; 2 × 550; 3 to 15 × 335; *after Gäumann*, 1922.)

marily endophytic, penetrate large areas of mesophyll, form knob-like haustoria of medium size and stimulate the leaves to form small galls. In time they push out between the epidermal cells, branch much there,

spread over the leaf surface and intertwine, forming chocolate brown to black, wooly coverings. These cling fast to the surface of the leaf by haustoria which, as in the Erysiphaceae, penetrate the epidermal cells, occasionally also by sinkers which bore between the epidermal cells (Fig. 130, 2).

Besides the usual vegetative hyphae, larger, more deeply staining hyphae, the sexual organs, also extend to the surface. The terminal cells are uninucleate (Fig. 130, 3 and 4). Originally they are both of equal size but later are differentiated into a slender male and a clavate female. They come into open communication with each other when the male nucleus migrates into the female copulation branch and fuses with the female nucleus. The unmated copulation branches develop again to vegetative mycelia (Fig. 130, 5 and 6). The zygote develops, as in the Erysiphaceae, to a short filament whose cells are all uninucleate, as far as known. The terminal cell is the largest and is very rich in protoplasm (Fig. 130, 9 to 11). The stipe cells are vacuolate and frequently undergo subsequent longitudinal division. When a filament has reached a certain length, it is surrounded by sterile cells from the stipe cell to the tip, and changes into a multispored ascus. The stipe cells collapse and the monascous perithecia finally lie free in the hyphal tissue (Fig. 130, 13). The peripheral cells of the sheath develop to long hyphae which (in connection with the mycelial hyphae?) surround the fructification like a wreath and finally intertwine in a hard crust (Fig. 130, 14). The spores mature only after the fall of the leaves; both this and the germination have not been investigated.

Lanomyces differs from *Sphaerotheca* in that the hypha growing from the ascogonium remains uninucleate throughout, goes through a complicated septation, changes its terminal cell to an ascus and causes the perithecial ground tissue to arise, not from the sporiferous hypha of the archicarp, but from the ascogenous hypha itself.

Besides, within the Perisporiaceae *Lanomyces* forms a noteworthy transition from endophytic to asterinoid growth. In the younger stages, the hyphae are entirely endophytic; later they develop predominantly on the surface of the leaf; similarly the copulation branches arise in the interior of the leaves but complete their development on the epidermis.

This transition from endophytic to asterinoid growth attains its complete development in the two following genera, *Balladyna* and *Meliola*. *Balladyna Gardeniae* forms sooty coverings on the leaves of *Gardenia* sp. in Java and stimulates them to manifold wrinkling and galls. The brown, epiphyllous, aerial mycelium grows radially and clings to the surface of the leaf by short, generally unicellar branches (**hyphopodia**) (Fig. 131, 1). Other multicellular branches with equally limited elongation are perpendicular to the surface of the leaf and project as rigid, vertical, pointed spines. A third kind of branch penetrates the mesophyll

through the stomata, and there forms numerous haustoria; these are reminiscent of the sinkers of *Phyllactinia* and are called **stomatopodia**; their development corresponds to that shown in Fig. 134 for *Parodiopsis;* only in *Balladyna* the haustoria are coralloid and almost fill the host cell, somewhat as depicted in Fig. 203, 3 for *Asterina Usterii* (Raciborski, 1900; Arnaud, 1918).

The perithecia arise from the clavate terminal cells of the branches of the aerial mycelium. In youth they are light brown, spherical; in age, brown, or black and ovoid. Their rind consists of a single layer of brownish, polygonal cells which at maturity become a greenish, almost hyaline slimy mass (Fig. 131, 2). The interior of the perithecium contains one, rarely two asci, each with eight dark, two-celled spores. *Balladyna* appears to hold a place among its relatives similar to that of

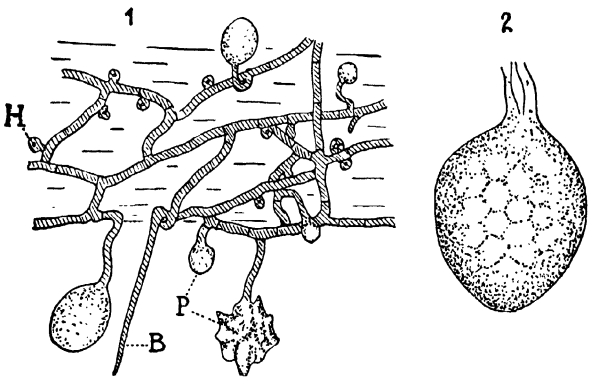


FIG. 131.—*Balladyna Gardeniae.* 1. Fungus mat showing hyphopodia, *H*, on the lower surface of a leaf, with setae, *B*, and young fundaments of fructifications, *P*. 2. Mature fructification. (× 250; *after Arnaud*, 1918.)

Sphaerotheca among the Erysiphaceae, in that neighboring forms, *e.g.*, the Javan *Alina Jasmini*, possess polyascous perithecia.

Meliola (Gaillard, 1892; Beeli, 1920; Doidge, 1920*a*, 1921; Ryan, 1926; Stevens, 1927) includes at present mostly tropical species (about 300), which form brown radiating mats on the under sides of leaves and fruits, rarely on young twigs. The asterinoid habit is already so marked that they are often considered epiphytes; in the more carefully investigated species, however, as *Balladyna* and the Erysiphaceae, they are ectoparasitic, sending knob-like haustoria into the epidermal cells and the tissue beneath (Maire, 1908; Doidge, 1921). As plant parasites they do not cause serious injury; however, some of them, as *Meliola Camelliae* and *M. Penzigii* on oranges and other citrus species, considerably diminish the value of the wares.

The hyphae are brownish black to brownish red; the growing parts and the parts which lie next the substrate are finer, lighter and thinner

walled, the more exposed superficial hyphae are more solid, thicker walled and darker. They form numerous sterile, rigid, very dark-colored spines (up to 1 mm. in length) which may be upright or bent over, simple, branched or forked, with a form often reminiscent of the appendages of *Uncinula* and *Microsphaera* in the Erysiphaceae. Accord-

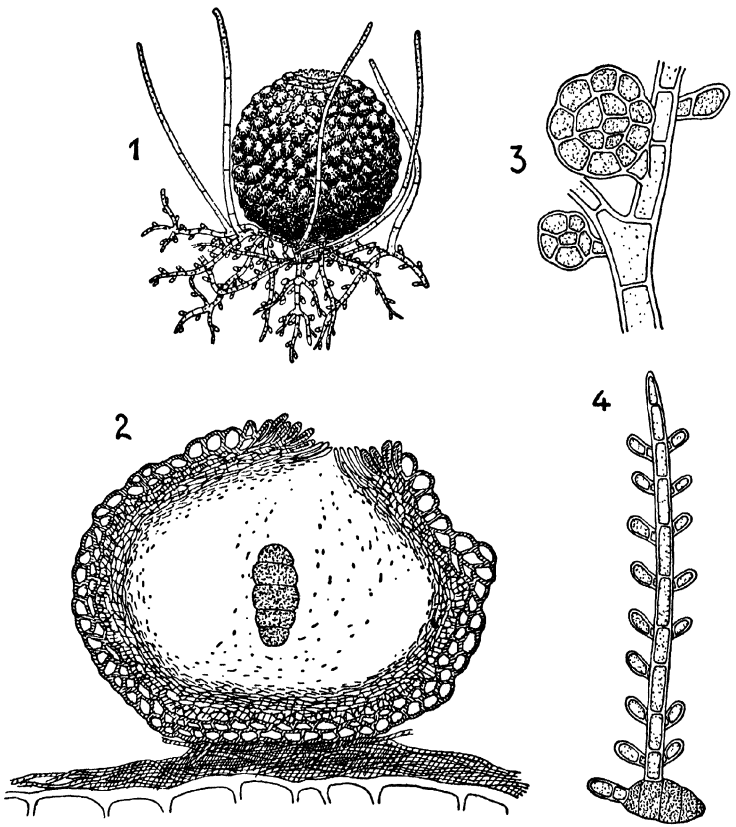


FIG. 132.—*Meliola corallina*. 1. Perithecium with hyphopodia and perithecial spines. 2. Median section of a mature perithecium which has discharged all ascospores but one. *Meliola evodiae*. 3. Mycelial branch with stigmopodia which develop perithecia. *Irenina obesa* (*Meliola obesa*). 4. Germ tube with hyphopodia. (1 × 100; 2 × 290; 3, 4 × 330; *after Gaillard*, 1892; *Bucholtz*, 1897.)

ing to the more or less frequent appearance of these mycelial spines, the mats are now thin and crustose, now thick and wooly; occasionally both aspects may occur side by side on the same leaf.

Besides these spines, the hyphae which tend to form perithecia in older mycelia, form hyphopodia. According to Gaillard, they may be divided into two types, the mucronate and the capitate types. The

mucronate hyphopodium (Fig. 132, 4) corresponds to the simple hyphopodia of *Balladyna;* they are mostly formed as two single, opposed cells which may be regarded as short, unicellular branches. Possibly they form the appressoria; their ontogeny is still unknown. The capitate hyphopodia or **stigmatopodia** (Fig. 132, 3) are generally darker than the mucronate hyphopodia and alternately branched; thus one cell forms one of these branches to the right, the next cell forms one to the left, the next to the right, etc. Generally the stigmatopodia are inclined obliquely forward toward the growing tip. They generally consist of two cells, a stipe cell and a spherical terminal cell, the **stigmatocyst.**

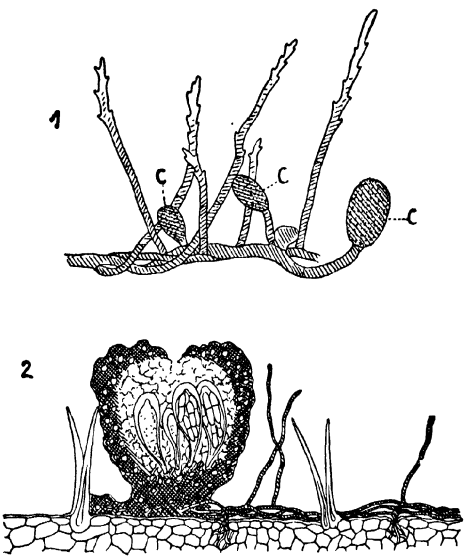


FIG. 133.—*Parodiopsis Perae.* 1. Hyphae with setae and young conidia, *C. Parodiopsis melioloides.* 2. Section through the lower surface of a leaf with setaceous mat and immature perithecium. (1 × 250; 2 × 100; *after Arnaud,* 1918, 1923.)

They are slightly reminiscent of the appressoria of the Erysiphaceae and possibly are related to haustoria.

The stigmatocyst may develop the perithecia; it swells and divides into two cells, the terminal cell developing slowly to form the core of ascogenous tissue while the basal cell produces the perithecium in a manner suggestive of that in the Laboulbeniales (Ryan, 1926).

Thus the perithecia, as in *Balladyna,* arise from a single branch of a hypha. At maturity they are spherical and resemble the Erysiphaceae; they consist of a dark, often carbonaceous rind, and a hyaline ground tissue, the rosette of asci. The brown rind is generally homogeneous, as in *Balladyna* and the Erysiphaceae; occasionally, as a step in the

direction of the Sphaeriales, it may become many layered. In many species, as in *Erysiphe* and *Leveillula* of the Erysiphaceae, it is symmetrical throughout the fructification; in others, as in *Microsphaera* and *Uncinula*, it is dorsiventral and is drawn out to a small wart or papilla at the tip; in other species, as in *Meliola corallina* (Fig. 132, 2), as a definite step in the direction of the Sphaeriales, a true opening, an ostiole, is formed at the top of the perithecium (Bucholtz, 1897). At times the perithecia, as in the Erysiphaceae, are provided with appendages, or perithecial spines, which, however, are only simple, unbranched and generally

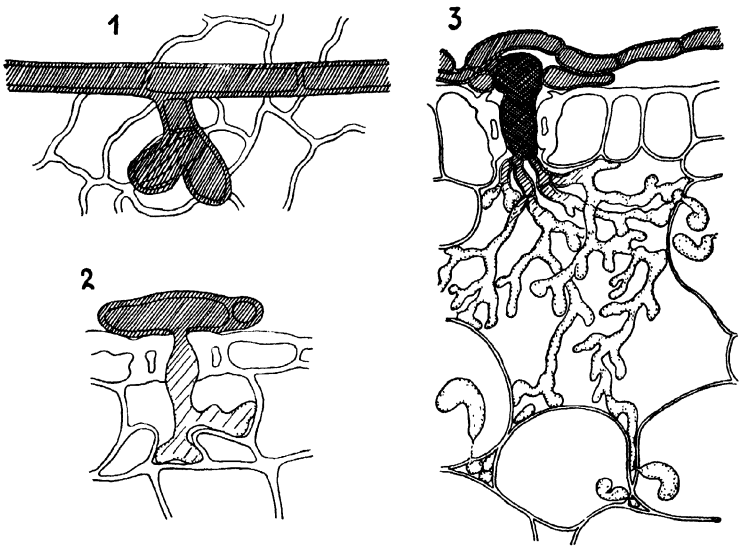


FIG. 134.—*Parodiopsis Stevensii*. Development of stomatopodia. 1. Seen from above. 2. In section (× 670). *Parodiopsis megalospora*. 3. Section showing intramatrical mycelium (× 530). (*After Arnaud* 1921, 1923.)

not numerous. Where complicated structures are described, there seems to have been a confusion with mycelial spines which rise below the perithecium.

The asci (another transition from the Plectascales to the Sphaeriales type) are generally spherical, rarely clavate. They usually contain only 2 to 4 brown, multiseptate spores.

From *Balladyna* and *Meliola*, the development proceeds in two directions, one blindly from *Balladyna* to the Englerulaceae, the other progressively from *Meliola* to the Sphaeriales. As we shall briefly discuss the Englerulaceae as a third family of the Perisporiales, the step to the Sphaeriales will be described here; it is completed by *Parodiopsis*. In this genus, the transitional character of the Perisporiales appears with

surprising clearness. In the arrangement of asci, *Parodiopsis* shows marked Perisporial characters; by the brown color and the behavior of the mycelium and by the possession of an ostiole it suggests the Amphisphaeriaceae of the Sphaeriales (Fig. 133, 2); and by the form and color of its perithecial wall, it would belong in the Hypocreales. As in both previous genera, the aerial mycelium emerges as a brown covering on the under side of a leaf and forms a liberal intramatrical mycelium through well-developed stomatopodia (Fig. 134). The perithecia are ochraceous, solid and generally rise above the stomata. If one imagines them entirely ingrown, so that the hyphal tissue in the stoma thickens into a prosenchymatous tangle, one has the Mycosphaerellaceae which we will discuss under the Sphaeriales.

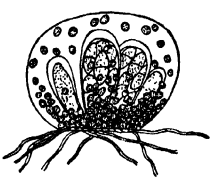


FIG. 135.—*Englerula Macarangae.* Immature perithecium. (× 130; *after Hoehnel*, 1909.)

Englerulaceae.—The only well-known representative of this family, *Englerula Macarangae* in East Africa, forms light brown coverings on *Macaranga* leaves (Hoehnel, 1909). In the young stage, the perithecia are spherical, without opening, and surrounded by a single-layered, brown rind formed of polyhedral cells. During the development of the three to five asci, the perithecial ground tissue gelifies. The gel is tough and swells much in water without dissolving. The outside of the perithecial wall differentiates a sharply defined, often nearly cuticular, slime layer.

The separation of the rind cells begins in the upper half of the perithecia so that, singly or in small groups, they are loosely imbedded in the slime or float upon it (Fig. 135). This process gradually continues, toward the bottom. At the bases this histolysis does not occur. Hence the mature perithecia are open above and surrounded by a hyaline, structureless gel into which the asci project.

The remaining representatives are less known than this species (Theissen, 1916*b*), hence an opinion as to their morphological relationships is not possible. Possibly they are connected to forms like *Balladyna.*

CHAPTER XV

MYRIANGIALES

The Myriangiales, like the Perisporiales, lead directly from the Plectascales, but their origin undoubtedly is more remote than that of the Perisporiales, perhaps at the stage of the Gymnoascaceae. If one imagines that the ascogenous hyphae of the Gymnoascaceae are longer so that they penetrate the whole hyphal mat which becomes compacted into a pseudoparenchymatous stroma, one has forms like primitive Myriangiales. These form pulvinate, irregular stromata in whose interior the asci are irregularly arranged in one or more layers; the ascospores are liberated only by the disintegration of the stromatal layers above them.



FIG. 136.—*Kusanoöpsis guianensis*. Diagrammatic section through a leaf showing two stromata. (*Stevens and Weedon*, 1923.)

Thus the Myriangiales (like the Perisporiales) are angiocarpous but at maturity every ascus lies embedded singly in the stromatal core, not tufted. The ascus chambers or cavities are called **loculi**.

As none of the forms have been studied cytologically, our morphological discussions in regard to the Myriangiales still lack ontogenetic bases. According to the differentiation of the stromata and the number of ascogenous layers, they may be divided into a series of families, five of which we will discuss here: the Myriangiaceae, Plectodiscellaceae, Saccardiaceae, Dothioraceae and Pseudosphaeriaceae. Their morphological relationships are given in the summary at the close of this order.

Myriangiaceae.—These are parasitic, more rarely saprophytic on leaves, bark and insects. Their distribution is chiefly tropical or subtropical. The consistency of their stromata is often suggestive of that of the Hypocreales, although in *Myriangium* itself they are more cartilaginous-gelatinous and generally brittle. According to the formation of the asci, they may be divided into two types. In one type, the asci are scattered irregularly over the whole stroma. In the other type they are

localized in definite regions of the stromata, *i.e.*, they are differentiated into sterile and fertile parts.

The first type may be illustrated by *Kusanoëpsis guianensis* in British Guiana, which on dicotyledonous leaves forms dark-colored pulvinate stromata, up to 1 mm. in diameter, erumpent from the interior of the host at maturity (Fig. 136). They lack a definite rind, although the pseudo-

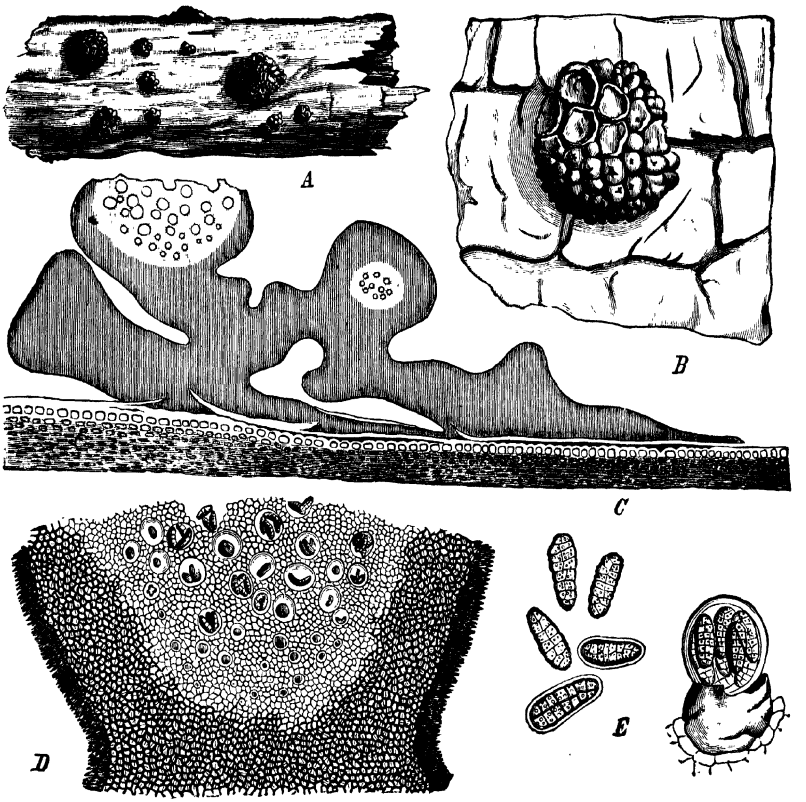


FIG. 137.—*Myriangium Duriaei*. *A*. Habit (natural size). *B*. Same (× 5). *C*. Section through an immature fructification (× 30). *D*. Section of conceptacle (× 100). *E*. Ruptured ascus and mature ascospores (× 250). (*After Millardet.*)

parenchymatous structure is always more marked in the sterile periphery than in the fertile core. The asci are spread in several layers over the whole interior, except the basal intramatrical portion, of the stroma, which projects like a foot into the mesophyll. The asci are spherical, the ascospores are hyaline and dictyosporic.

The second type is shown by *Myriangium* (*Phymatosphaeria*). The majority of its species are parasitic on insects, especially plant lice. Like

the foot in *Kusanoöpsis*, this second type spreads over the substrate in a sterile stromatic plectenchyma, which, in the forms on animals, as *M. Duriaei* may be pulvinate, the stromatal hyphae being sclerotic and narrow lumened (Fig. 137, *C*); those on plants, as in *M. Pritzelianum*, form only a thin membrane of hyphae with unthickened walls. The cells on the surface of the stroma become brown and change to a dark, otherwise undifferentiated, rind.

From this sterile basal stroma arises a tuft of numerous vertical processes like a small pezizoid group (Fig. 137, *A* and *B*). They consist of the same plectenchymatous ground tissue as the basal stroma. They form the spherical asci in an apical, sharply defined, patelliform zone.

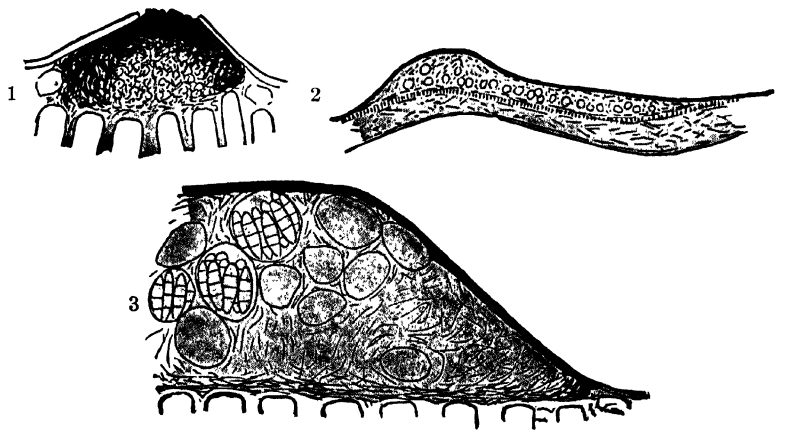


FIG. 138.—*Plectodiscella Pyri*. 1. Section through fundament of a stroma. 2. Stroma which has already ruptured the cuticle. 3. Section through a mature stroma. (1, 3 × 500; 2 × 82; *after Woronikhin*, 1914.)

As in *Kusanoöpsis*, these are arranged in several layers (except in the Singhalese *M. Thwaitesii*) and contain hyaline dictyospores, liberated by the crumbling of the peripheral stromatal layers. As this crumbling proceeds more rapidly in the middle than at the edges, the mature ascigerous parts seem more like an apothecium. Occasionally, when the vertical portions are absent, the flat basal stromata form the asci in their own apical portions (Petch, 1924).

Myriangium forms only one branch of the Myriangiales and as such ends blindly, hence the ontogenetic connections of the higher families should be sought in the simpler Myriangiaceae, with undifferentiated stromata similar to *Kusanoöpsis*. From this point, development has probably proceeded in two directions, one to the formation of special coverings of the stromata, the other to the reduction of the number of asci and their arrangement in a single layer.

Plectodiscellaceae.—The first type is realized in *Plectodiscella Pyri* (Woronikhin, 1914) causing a leaf spot of apple and pear in the Caucasus. The young fructifications arise between epidermis and cuticle as a ball of closely intertwined hyphae colored light at the base, but brown on the upper side and at the edges. By the further development of this ball into a pulvinate stroma, the cuticle is ruptured and the young fructification is more or less exposed. In contrast to *Kusanoöpsis*, there are special rind layers (Fig. 138, 3). The underside remains a hyaline, compacter, more-marked pseudoparenchyma than the core of the stroma. The upper side is brown, and develops to a strong, sclerotic, outer layer consisting of polyhedral cells and uniting at the base of the stroma with the basal rind layer. At maturity the outer layer breaks off and after it the stromatic ground tissue, liberating the hyaline 4-celled ascospores. A second species, *Plectodiscella veneta* (Burkholder, 1917), which causes anthracnose of *Rubus* in the United States, is noteworthy in that the ascospores under definite conditions of nourishment germinate first to a sprout mycelium. As an imperfect form, the Melanconiaceous *Gloeosporium venetum* occurs.

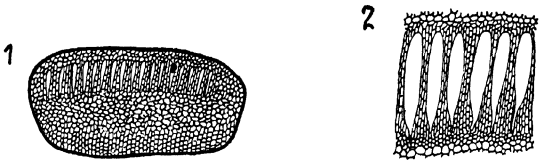


FIG. 139.—*Bagnisiella australis*. 1. Section through the stroma from the bark of the host, 2. Same, further enlarged. (*After Theissen and Sydow*, 1915.)

Saccardiaceae.—In this family, in contrast to the lower Myriangiaceae, is realized the second possibility, the reduction of the number of asci which are no longer formed irregularly in several layers but in a single layer generally lying directly beneath the surface of the stroma and parallel with it (*mutatis mutandis* as in *Myriangium Thwaitesii*). The Saccardiaceae include a whole series of chiefly monotypic genera, as *Eurytheca*, *Saccardia* and *Anhellia;* these are incompletely known and generally have been studied only in herbarium material. One may easily acquire an idea of their structure, however, if one imagines the asci of *Kusanoöpsis* in Fig. 136 to be arranged in a single layer.

Dothioraceae.—Among the simpler genera, as in *Bagnisiella* (ascospores unicellular) and also in *Dothiora* (ascospores muriform), we may sider *Bagnisiella australis* which forms its stromata in rows in the bark of dead branches of *Acacia bonariensis* in the Argentine; like those of the previous families, they are still indefinite in form, pulvinate, always surrounded with a special, dull black, crust-like rind (Fig. 139, 1). Their new covering behaves like the asci and ascigerous layer. In contrast to most Saccardiaceae, the asci are no longer spherical as in the

Plectascales, but elongate-clavate; they are pressed together in a palisade and force the stromatic ground tissue, the so-called interthecial stroma (Fig. 139, 2) together to paraphysoid filaments, the pseudoparaphyses or paraphysoids (terminology of Petrak, 1923). The **paraphysoids** differ from paraphyses in that, as the remains of the interthecial stroma, they have a cellular structure and do not terminate freely but continue further into the pseudoparenchymatous cover tissue.

In the higher Dothioraceae, as in *Bagnisiopsis*, there appears, as in the Myriangiaceae, a tendency to limit the asci to definite, narrowly limited conceptacles which are differentiated out of the interior of the stroma (Fig. 140). The dull black, pulvinate stroma of the Brazilian *Bagnisiopsis peribebuyensis* is erumpent from the leaves of various Melastomataceae dotting their surface with small papillae. In contrast to *Bagnisiella*, the asci do not form a continuous layer but are localized in sharply defined nests which, like the fertile parts of *Myriangium*, are generally surrounded by a darker tissue. They lie singly (as in *Bagnisiella* and the other Myriangiales) in special loculi and are separated from each other

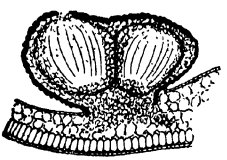


FIG. 140.—*Bagnisiopsis peribebuyensis*. Section of mature stroma with two ascigerous conceptacles. (× 33; *Arnaud*, 1921.)

by thin stromatal layers. With this spatial limitation of the asci, the whole stromatal cover does not degenerate at maturity but small parts, which have lain directly over the conceptacles, crumble and form an irregular pore through which the ascospores escape (Fig. 140, left).

During further development of the Dothioraceous line the single conceptacle is gradually individualized. Like the fertile branches of *Myriangium*, they sprout from the sterile stroma, thereby acquiring their own wall while sterile stroma becomes more and more limited to the intramatrical part.

This development may be followed in *Botryosphaeria* (Theissen and Sydow, 1915; Theissen, 1916; Hoehnel, 1920). The simpler species, as *B. inflata* (Fig. 141, 1) appear entirely like *Bagniopsis* but occupy a partly lower stage, for their conceptacles are scattered irregularly over the stroma and are still entirely imbedded in the plectenchyma; at maturity their tips project only a little beyond the stroma and hence hardly raise the bark of the host. In other species, as *B. Viburni* (Fig. 141, 2 and 3), they gradually collect and arch toward the surface of the stroma; but still, according to the luxuriance of the stromata, they may be surrounded by the plectenchyma entirely or only to half their height.

In *B. mascarensis* (Fig. 141, 4) they develop entirely above the surface of the stroma upon which they rest at maturity; hence these are true, sterile, basal stromata, as in *Bagnisiopsis peribebuyensis*. Along with this development, there has been a fundamental alteration in the course of the stromatal hyphae. While in the lower forms, as in *B. inflata*, they still run entirely irregularly, in the higher forms they have become increasingly vertical and finally run parallel from the base to the top of the stroma.

In the highest stage, as in *B. Bakeriana*, *B. Quercuum* and *B. Ribis*, the stromata begin to buckle and split between the conceptacles which are left standing on shorter or longer stipes and have their own walls, *i.e.*, they become perithecia.

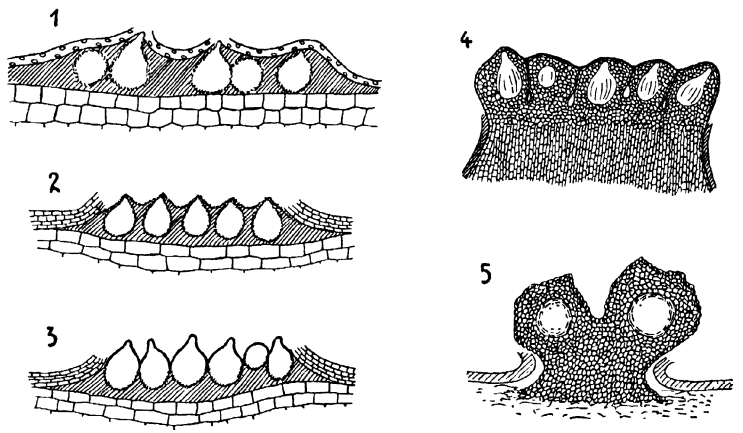


FIG. 141.—Development of stroma in *Botryosphaeria*. 1. *B. inflata*. 2, 3. *B. Viburni*. 4. *B. mascarensis*. 5. *B. Bakeriana*. (*After Theissen*, 1916.)

B. Quercuum (*Melanops Quercuum*) forms its brown stromata on oak bark between the periderm and the bark parenchyma beneath and pushes out the periderm which it ruptures with radial splits, so that the peridermal lobes remain like steep walls. Meanwhile it has grown higher, but seldom to such a degree that it projects over the peridermal lobes. As in *Myriangium*, there develop columnar outgrowths which broaden spherically above and end at the top with a conical papilla. This conceptacle tissue is, as in the other Dothioraceae, entirely like the basal stroma in structure and is continuous with it. The spherical head portion is also a pseudoparenchymatous mass. In it, a hyaline spherical conceptacle, containing a palisade of monascous loculi, is differentiated. The paraphysoids are occasionally not only pressed together into threads but also dissolved so that the asci are embedded in a gel. In this condition, the conceptacle appears entirely like the true perithecium and only its ontogeny shows its Myriangial character.

At maturity the papillae break off and the conceptacle parenchyma, possibly still present over the asci, is dissolved so that the tips of the asci are free. As *Meliola* and *Parodinopsis* of the Perisporiaceae, so also *Botryosphaeria* of the Dothioraceae has perithecia whose place of opening is typical. They do not, however, open by pores but by histologically differentiated parts of the stroma which, because of the formation of dehiscence zones, are more easily crumbled away.

B. Ribis causes the currant cane blight (Grossenbacher and Duggar, 1911; Shear, Stevens and Wilcox, 1925). In July the first conidial forms (in the imperfect genus *Macrophoma*) appear on the withering young shoots; in the following spring there break forth from the dead branch

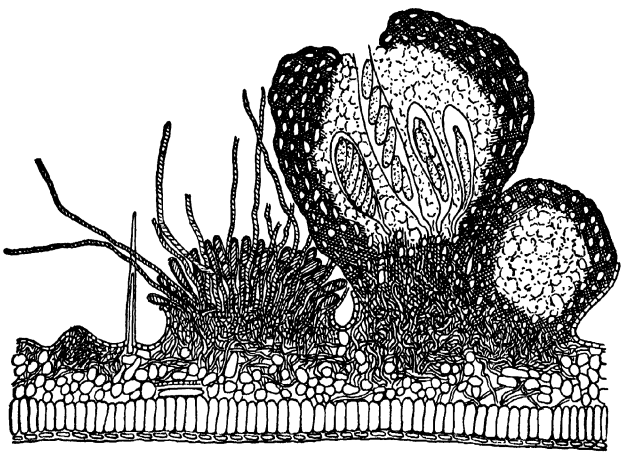


FIG. 142.—*Parodiellina manaosensis*. Section through lower surface of leaf with conceptacle and setaceous conidial stroma. (× 110; *Arnaud*, 1921.)

numerous black stromata which first bear the pycnidia of the second imperfect form, *Dothiorella*, and later swell with the perithecia.

This type of the highest species of *Botryosphaeria* appears again in the Dothioraceae with many modifications. In *Parodiellina manaosensis* on the under side of leaves of Brazilian Solanaceae, two stromata break out, one of which cuts off dark brown, uni- or multicellular conidia, while the other bears perithecioid conceptacles (Fig. 142). The stroma surrounding these conceptacles consists of solid cells and is an intense reddish brown. When young, it is entirely closed, but at maturity gradually crumbles at the top. The ascigerous stromatal parts seem extraordinarily like the fertile branches of *Myriangium*, especially if one imagines the basal stroma in Fig. 137 less well developed, as is actually the case in many species, except they are more individualized with consequent reduction in number of asci.

This individualization of conceptacles is greater in the West African *Chevalieropsis ctenotricha* (*Chevalieria ctenotricha*) (Fig. 143); here the poorly developed echinate stroma forms several conceptacles which are only attached to the stroma by a narrow base. In several adjacent loculi, they contain a few, narrow, clavate asci, each of which normally forms 8 two-celled ascospores. At maturity, the pseudoparenchyma at the top of the conceptacle becomes slimy and the ascospores are liberated through this slime, apparently as in the Englerulaceae.

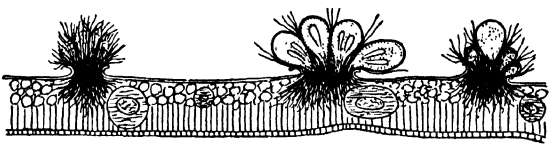


FIG. 143.—*Chevalieropsis ctenotricha.* Section through a dicotyledonous leaf with several conceptacles. (× 33; *after Arnaud*, 1921.)

With *Chevalieropsis*, *Parodiellina* and *Botryosphaeria*, we have temporarily finished with a special branch of the Myriangiales, which we shall meet later in the families of the Dothideales and Sphaeriales.

Pseudosphaeriaceae.—As the starting point of the last family of the Myriangiales to be discussed here, we must go back a few steps in the Dothioraceae to the stage of *Bagnisiella* and *Dothiora*. While the true Dothioraceae branching off from these two genera retain their broad pulvinate stromata, and only differ in that the conceptacles grad-

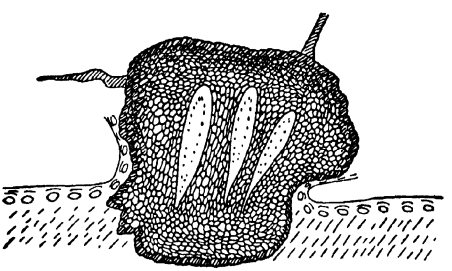


FIG. 144.—*Pyrenophora trichostoma.* Section of young stroma. (*After Theissen*, 1916.)

ually lie on the upper surface of these cushions, the Pseudosphaeriaceae develop in the direction of reducing the basal stromata to one conceptacle. In both families there is a tendency toward the individualization of the conceptacle; in the Dothioraceae it is shown by the raising of the conceptacles over the stroma and by a gradual degeneration of the remaining stroma, while in the Pseudosphaeriaceae it is realized by the degeneration of the whole stroma. By this degeneration and spatial limitation of all the stromata, they attain in the Pseudosphaeriaceae a characteristic form and become as a whole true independent fructifications,

while in the higher Dothioraceae, one would rather consider the single conceptacle-bearing branches which grow out of the stroma as fructifications. From the perithecia of the Perisporiales (and of the Sphaeriales), these fructifications of the Pseudosphaeriaceae, except for the special question of opening, are distinguished by the fact that in the former the pore tissue of the perithecium is entirely resorbed during development while in the latter, as in all the other Myriangiales, it remains as interthecial pseudoparaphyses (Hochnel, 1909; Theissen, 1916; Theissen and Sydow, 1918; Petrak, 1923).

An illustration of the fructification of this family is shown in *Pyrenophora* (Fig. 144) and *Pleospora* (Fig. 145, 1). The fructifications are small and like perithecia; they are immersed in the host and liberated by

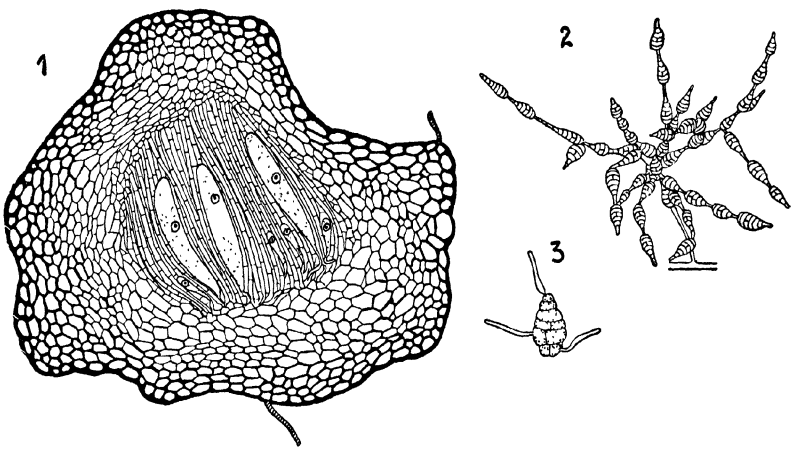


FIG. 145.—*Pleospora herbarum*. 1. Section through an immature perithecium (× 250). 2. Conidiophore (*Alternaria* type) (× 135). 3. Germinating conidium (× 235). (*After Arnaud*, 1918, *and Brefeld*, 1881.)

the rupture of the epidermis. They consist of a pseudoparenchyma which is thick walled and dark colored in the two or three outer layers of cells (outer crust) but on the inside has a more delicate structure. In the middle of the stroma, each of the elongate asci develops in its own core cavity. By the increase of asci in the course of development, the intermediate hyphal bundles are compressed as far as possible and finally remain only as thin, flabby paraphysoids merging into the stromatic cover. The top of the perithecium eventually becomes more or less markedly papilliform. It opens by the crumbling and falling away of the papillae, giving the appearance of opening by a round pore.

While in *Pyrenophora* at present only saprophytes are known, *Pleospora* (numbering about 300 sp.) includes several plant pathogens, as *P. herbarum* on many stems and fruits, *P. Hyacinthi*, the cause of the

black disease of hyacinths, and *P. gramineum* which causes the stripe disease of barley; their imperfect forms belong to *Cladosporium*, *Alternaria* and *Macrosporium* (Fig. 145, 2), and in *P. gramineum* to *Helminthosporium*. In a special form of *P. herbarum* causing a leaf spot of *Livistonia australis* (*Corypha australis*) Cavara and Mollica (1907) have demonstrated that the hyphae are uninucleate. From two hyphae, two unicellular branches are formed which, as in *Penicillium "crustaceum"* and *Sphaerotheca Humuli*, approach, embrace and copulate. Meanwhile they have become surrounded by sheath hyphae and later develop ascogenous hyphae in an unknown manner. As sparse as this evidence is, it may be assumed that the Myriangiales have still retained the Plectascales type in the form and function of sexual organs.

Pleospora and *Pyrenophora* have until recently been assigned to the Sphaeriales and only a special investigation of their young perithecia has demonstrated their undoubted Pseudosphaeriaceous character. Besides these, however, a series of genera, as *Meliola* and *Parodiopsis* in the Perisporiaceae and as *Parodiellina*, *Chevalieropsis* and *Botryosphaeria* in the Dothioraceae, show marked transitional forms which might be with equal justice classified in the family in which they root, in this case the Pseudosphaeriaceae, as in the group to which they lead, in this case the Sphaeriales. *Didymella* and *Leptosphaeria* will be discussed here.

Didymella has 200 species parasitic or saprophytic on the roots and dry leaves of cormophytes. In structure of fructifications they develop from the simpler forms similar to the *Pleospora–Pyrenophora* type, through numerous transitions, to another extreme which extends into the Sphaeriales. In the simpler forms, as in *D. moravica* and *D. proximella*, the perithecia, as in *Pleospora* and *Pyrenophora*, are still entirely enclosed and open only at maturity by the crumbling of the more or less sharply defined tip. In this form, the interthecial plectenchyma is generally still present at maturity in the form of distinctly recognizable paraphysoids. In the higher forms, as in *D. Rehmii*, *D. cladophila* and *D. applanata*, the cause of a "brush" disease of raspberries, the perithecia attain a more or less characteristically formed opening, an ostiole, which we meet again in the majority of the Sphaeriales.

Besides, in them the perithecial stroma is only weakly developed and generally only present at maturity as a scant hyaline mass which easily swells in water. While *D. moravica* and its relatives belong to the Pseudosphaericaceae, the *D. Rehmii* group considered by itself would be placed in the true Sphaeriales.

This transitional character is still more marked in *Leptosphaeria*, whose species show the characters of not less than three orders, the Myriangiales, Dothideales and Sphaeriales, and hence has been divided by most authors into different genera, which in practice are difficult to distinguish.

The simple species of *Leptosphaeria* correspond in structure of conceptacles and perithecia to *Pleospora*, and since *Pleospora* still is counted in the Sphaeriales, they were placed in the same family with it. In a few of them, as in *L. doliolum*, on the roots of the larger weeds, especially *Urtica* and *Angelica*, the conceptacles, as in *Pleospora*, are still closed in youth. They do not open by the crumbling of the papilla, however, but by partial slimy resorption of the lid tissue whereby at maturity a typical pore results. In both *Pleospora* and the *L. doliolum* group, the paraphysoids are long-celled filaments and, when mature, almost indistinguishable from typical paraphyses. In *Leptosphaeria acuta* on *Urtica dioica* and *L. herpotrichoides* causing the increased fragility of stalk in young shoots of rye, a typical ostiole pierced by a canal is formed organically in the course of development, as in the true Sphaeriales; furthermore, the species of this group, like the true Sphaeriales, have true paraphyses formed by subsequent growth of the hyphae of the ground tissue.

While *Leptosphaeria doliolum* and *L. acuta* mark the beginning and end of a series which leads from true Pseudosphaeriaceae to true Sphaeriales (*i.e.*, the forms among these with discreet perithecia) a special branch of the *Leptosphaeria* group connects directly to *Botryosphaeria* and leads thence to the stromatic Sphaeriales and Dothideales. Not only do these genera merge in the vertical direction, but also horizontally and laterally. Hence it is difficult to decide whether this stromatic branch of the *Leptosphaeria* group (in the developmental scheme on p. 223 imagined as the left wing of *Leptosphaeria*) should be joined with forms having discrete fructifications which appear to be perithecia and show no traces of stromata, or whether they would not be better placed in a special genus of the Dothioraceae beside *Botryosphaeria* or, as Hoehnel (1918) wishes, shifted to the Dothideales.

This left wing connects directly to the solitary species, through forms whose perithecia are gregarious only under favorable conditions of nourishment. In the higher forms as in *Leptosphaeria caespitosa* on the dry roots of *Artemisia campestris*, or *L. salebrosa* on decaying cabbage stumps, the perithecia appear evenly on a basal stroma which is often only weakly developed. If the basal stroma is more strongly developed and the conceptacles are caespitose, the mat ruptures during the epidermal development, *i.e.*, before the conceptacles are externally visible, and the fungus attains instantaneously an entirely different appearance, suggestive of the higher species of *Botryosphaeria* and *Chevalieropsis*. If one imagines this basal stroma more strongly developed, one has *Rosenscheldia* which, according to present systematic classification, is placed in the Dothideales. Thus *L. doliolum* and *L. acuta* form the beginning and end members of the Pseudosphaeriaceae–Sphaeriales series and *L. caespitosa* and *Rosenscheldia* two stages in the line of development from the Pseudosphaeriaceae to the Dothideales.

Unfortunately the species of *Leptosphaeria*, as all other Myriangiales, have been only incompletely investigated ontogenetically. Only for *L. Lemaneae*, on the fresh water red alga *Lemanea*, has Brierley (1913) observed that, as in *Pleospora* and *Penicillium "crustaceum,"* at the formation of the perithecia, two hyphal branches embrace each other and come into open communication at the tips; it seems, however, that copulation may also occur without this helix formation between two extended hyphal branches. Many species of *Leptosphaeria* are important as causes of plant disease. The *L. avenaria* group, on numerous species of grasses, are related to each other but differ in their conidial dimensions and biologically according to their choice of host; their imperfect forms belong to *Septoria* (Weber, 1922, 1923). *Septoria secalis*, for example, is specialized on *Secale cereale*, *S. Passerinii* on *Hordeum* sp., *S. Agropyri* on *Agropyron repens*, *S. Bromi* on *Bromus inermis*, *Leptosphaeria avenaria* on *Avena*. Two other species have somewhat less specialized hosts, as *Septoria tritici* and *S. nodorum* which both infect *Secale cereale*, *Triticum* sp. and *Poa pratensis*.

Summary.—The special distinction of the Myriangiales is that every author circumscribes and divides them differently; they are an order of transitional forms showing connections in all directions, but the further we go into their ontogeny the more they seem to be the key group to the higher Ascomycetes.

As far as an interpretation may be based on the morphological relationships of mature fructifications, there are presented in the following diagram the relationships between the individual Myriangeles as the author conceives them; it is obvious here, as in all diagrams of this type, that we deal with types, not genera or species.

The Myriangiales form the starting point with a massive, homogeneous, often highly colored stroma, in which the spherical asci lie

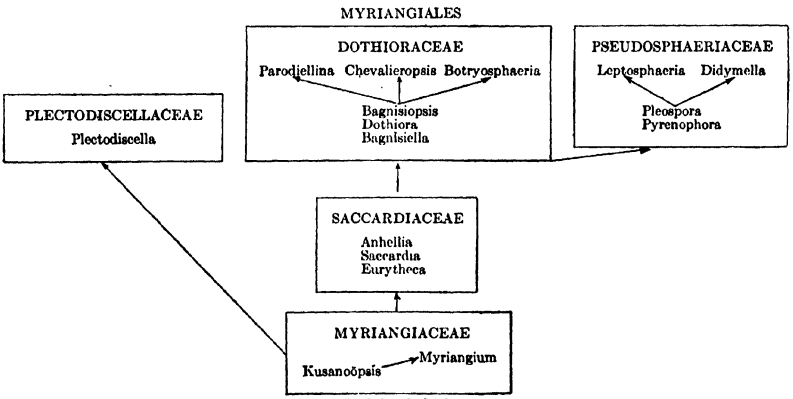


DIAGRAM XXII.

irregularly scattered. In them are the germs of two characteristic groups which are significant for the later development of the whole order. On the one hand, there is the differentiation of the stroma into a fertile and sterile part (*Kusanoöpsis–Myriangium* series), on the other the localization of the asci into a single layer (*Myriangium Duriaei–M. Thwaitesii*).

The further development of the Myriangiales takes place in the two directions marked by the families of the Plectodiscellaceae and Saccardiaceae. In the Plectodiscellaceae the irregular arrangement of the asci is retained; the stromata, however, form a special rind crust which develops on the upper side to a true cover plate. In the Saccardiaceae, however, the original irregular arrangement of the asci is lost and is replaced by a single palisade-like ascigerous layer; the homogeneous structure of the stromata, characteristic of the Myriangiaceae, is retained in them; the formation of a rind crust or cover plate is notably absent.

By an increase in number and elongation of asci (transition from spherical to clavate form) the Saccardiaceae may have given rise to the lower Dothioraceae, whose stromata, indefinite in form, as in the Saccardiaceae, are pulvinate, but whose interthecial stroma has become compressed to thread-like pseudoparaphyses by the maturing asci. Besides this degeneration of the interthecial core, there appears a tendency in the lower Dothioraceae, as in the *Kusanoöpsis–Myriangium* series of the Myriangiaceae, to differentiate the stromata into sterile and fertile parts, *i.e.*, to restrict ascus formation to definite fertile parts, the conceptacles, which become increasingly independent.

This individualization of conceptacles has proceeded in two directions. Each stroma of the higher Dothioraceae develops several conceptacles which gradually emerge from the stromatal surface, finally dividing it into a sterile basal stroma and a sessile, external fructification, the perithecium. In the Pseudosphaeriaceae only one conceptacle is formed in each stroma, which is reduced to a single perithecium. In both the higher Dothioraceae and the Pseudosphaeriaceae the individualization of the conceptacles and formation of a special perithecial wall is accompanied by a gradual differentiation of an ostiole, also by an entire gelification of the interthecial ground tissue and the formation of true paraphyses. As a result of these two developmental processes, the forms entirely lose their Myriangial character and join the higher orders.

In these varied developmental forms lie the roots of a whole series of higher Ascomycetes. Hence in no less than five different orders, the Sphaeriales, the Dothideales, the Hemisphaeriales, the Phacidiales and the Pezizales, we will have to refer to the relationships of the Myriangiales.

CHAPTER XVI

HYPOCREALES

The Hypocreales are generally defined as Pyrenomycetes with a soft (not hard and carbonaceous and hence not brittle), brightly colored (white, yellow, red, violet or light brown) perithecial wall. Where systematic relationships are firmly established, occasionally we include dark-colored or hard-walled forms, such as *Ophiodotis*, *Entonaema* and *Xylocrea*, which according to the definition would belong to the Dothideales or Sphaeriales.

There are so many Hypocreales that it seems impossible to give a satisfactory systematic classification. Lindau (1897) and Seaver (1910) use as the fundamental principle, the behavior of the perithecia, whether they are solitary or united in slightly or highly differentiated stromata; they realize, however, that the consistent following of this principle separates parts of the same natural genus among entirely different families. In order to lessen this difficulty, which would be very serious in the present work, we have used the septation of ascospores as the only principle of division, as advocated by Saccardo in the *Sylloge Fungorum* and by Möller (1901). Thus we have divided the genera selected for discussion here into three groups: the first contains the Amerosporeae (ascospores unicellular); the second includes the Didymosporae (ascospores bicellular), the Phragmosporae (ascospores tri- and multicellular) and the Dictyosporae (ascospores reticulately septate); the third contains the Scolecosporae (ascospores filamentous, unicellular at first, becoming multicellular).

It is obvious that this classification is entirely artificial; it has the advantage, however, that there is rarely any doubt as to where one should seek a genus. Further, it seems that the Scolecosporae, at least, form a more natural group because of the behaviour of their ascospores; their asci are always long, slender and fine and, as far as known, always have a characteristic cap with a thread-like canal. It is possible that this peculiar structure of the ascus is older and more important for a natural systematic classification than the morphology of the spores.

The Amerosporae may be divided into three stages, the first, in which the perithecia generally stand singly on the substrate, the second, in which they are united in undifferentiated cushions and the third, in which these pulvinate stromata develop into specially formed fructifications. Of the first group, we will cite here four genera, *Melanospora*,

Neurospora, *Peckiella* and *Neocosmospora*. *Melanospora* and *Neurospora* are saprophytic on many decaying substrates of both animal and plant origin, and parasitic on other fungi. On their substrate they form a brownish or whitish, often felty tissue; occasionally the hyphae intertwine to form an enormous mass of small bulbils which, where the perfect form is unknown, are assigned to the imperfect genus *Papulaspora* (Hotson, 1912). Vincens (1917) regards these bulbils in part as undeveloped perithecia.

Melanospora Mangini, *M. globosa* and *Sphaeroderma bulbillifera* have unicellular, hyaline conidia borne in chains on small phialides (*Oospora* or *Spicaria* type). *M. marchica*, *M. globosa* and *Sphaeroderma bulbillifera* also form dark-colored gemmae or bulbils, whose forms are reminiscent of the smut spores of *Tuburcinia*.

As in the Aspergillaceae, *M. parasitica* (Kihlman, 1883) and *M. Zobelii* (Nichols, 1896), parasitic on other fungi, and the saprophytic *M. marchica* (Neger, 1914) form two copulation branches which, as in *Aspergillus nidulaus*, intertwine helically. The saprophytic *M. globosa* and *Sphaeroderma bulbillifera*, as in *Aspergillus herbariorum*, form a helical ascogonium up whose side the antheridium climbs. The cytological relationships are unknown; apparently the asci, at least in *M. parasitica*, *M. Zobelii* and *M. Mangini*, do not arise from ascogenous hyphae but a cell of the ascogonium divides in all three dimensions and the asci develop from cells of this complex. The hyphal cells are multinucleate.

The mature perithecia generally have a one-layered wall and a very long neck, through which the brownish spore mass is pressed, following the degeneration of the asci. The hyphal felt under the perithecia thickens to a subiculum, then to a loose and finally to a fleshy stroma, on which rest the perithecia singly or in groups.

Neurospora, which differs from *Melanospora* by black perithecia, absence of the long, fimbriate beak and its persistent asci, shows some resemblance to the Sordariaceae. *Melanospora Mangini* and related species show many characters in common with this genus and perhaps should be considered here rather than in *Melanospora*, where they form a very aberrant type. *Melanospora destruens* (Shear, 1917), on cranberries, also shows many characters similar to those of this genus. The conidial stages of *Neurospora sitophila* have usually been referred to *Monilia sitophila* or related species which appear as cushions of orange to pale salmon, oidia occasionally causing severe damage to the baking industry.

The development and cytology of this group has been little studied except for the reports of Möller (1901), although an extensive investigation is in progress by B. O. Dodge. *Melanospora Mangini* (Vincens, 1917) and *Neurospora erythraea* form only one copulation branch, originally three to five celled (as in *Aspergillus flavus* and *A. fumigatus*), which coils helically or in an irregular tangle and is surrounded by sheath

hyphae in the usual manner. The perithecia are gregarious or scattered, smooth or with loose hairs, the cavity lysigenic, filled at first with parallel septate hyphae which disappear as the young asci expand; the ascospores become black or greenish black and longitudinally ribbed. *N. erythraea* is apparently homothallic, while *N. sitophila* and *N. crassa* are heterothallic (Shear and B. O. Dodge, 1927). In *N. tetrasperma*, the spores vary much in size depending upon the number produced in an ascus. Ordinarily there are four spores, but occasionally five to six or two to three are produced. Cultures from the large spores are homothallic, while those from the small spores are heterothallic. The spindle of the first division in the ascus lies along the long axis, hence the daughter nuclei migrate toward the ends of the ascus. In the second division, the spindles are longitudinal or in about half the cases, oblique and appear to be dividing conjugately, hence the nuclei finally appearing at the ends of the ascus are non-sister nuclei. In the third division, the spindles are transverse and the adjacent non-sister nuclei unite in cutting out a large homothallic spore. This is followed by subsequent slipping and turning of the spores, since at maturity they lie in a single row. In the uninucleate heterothallic spores, the relations of the spore nuclei are not clear, but in *N. crassa* and *N. sitophila*, the adjacent, uninucleate spores are always developed from sister nuclei (B. O. Dodge, 1927). In these species, where there is little chance for shifting, further studies by B. O. Dodge and Wilcox will probably locate conclusively in which division of the ascus the segregation of sex occurs.

Peckiella is parasitic on pileate fungi and morphologically corresponds to *Hypomyces* of the Didymosporae; only their ascospores are unicellular. On the under side of caps of *Lactarius deliciosus*, *P. lateritia* forms a stroma thick enough to cover the lamellae. As in *P. Thiryana* (Maire, 1905), which has also been investigated in this respect, the hyphal cells are uninucleate. As in *Melanospora Mangini* and *Neurospora erythraea*, only the ascogonium is formed. It curls twice at the most. Its cells undergo repeated divisions but always remain uninucleate. Later, by nuclear divisions which are not followed by septum formation, they become binucleate and develop to ascogenous hyphae which form asci according to the hook type (Moreau, 1914).

Neocosmospora vasinfecta will only be mentioned here because it is erroneously considered the cause of a wilt of cotton and of watermelons and is occasionally described as such in the literature of plant pathology. Its perithecia, like those of the simpler species of *Melanospora*, arise singly on the substrate and are colored a brilliant red (Butler, 1910).

The second stage, in which the perithecia are united on undifferentiated pulvinate stromata, is shown by *Entonaema* and *Polystigma*. As *Polystigma* is known cytologically and hence affords opportunity for a special discussion, we will return to it at the end of the Amerosporae

after finishing the third group. *Entonaema liquescens* (Fig. 146) in the primeval forests of Brazil, forms light-colored, soft gelatinous, vesicular fructifications, suggesting *Tremella*, attaining a diameter up to 40 cm. and a height above the substrate up to 15 cm. Under this light-colored outer layer lies a deep black plectenchyma in which, over the entire fructification, are embedded the perithecia. Because of this dark color of the deeper tissues, which in another species, *E. mesentrica*, extends to the outer layers, and because of the dark color of the ascospores, the author of this genus assigned them to the Xylariaceae under the Sphaeriales. There, however, its position is entirely isolated while it easily fits in the Hypocreales. The dark color of the

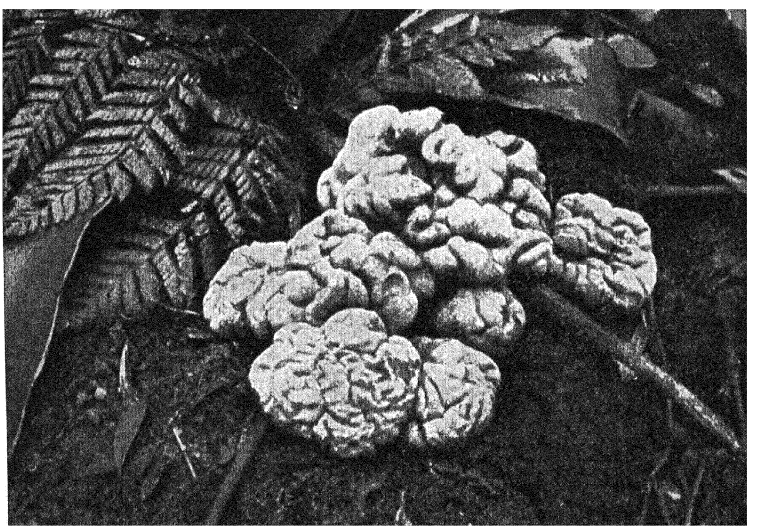


FIG. 146.—*Entonaema liquescens*. Habit of perithecial stroma (× ⅙; *after Möller*, 1901.)

tissue does not necessarily argue against its classification in the Hypocreales, as many unquestioned representatives of *Hypocraea* and *Hypocrella* show an equally dark color of the rind or the deeper plectenchyma of the perithecial walls. The dark color of the ascospores is common to *Entonaema* and *Melanospora*.

The third stage is represented by *Xylocraea*, in which the perithecial stromata develop elaborate fructifications. *X. piriformis*, on wood in Brazil, forms fructifications like those shown for *Mycomalus* in Fig. 159, except that it is pyriform instead of maliform. Furthermore, their perithecia are not formed over the whole surface but only in a limited region at its thicker end, corresponding to the blossom end of the pear.

In contrast to all these genera, *Polystigma* is parasitic on angiosperms. Its best-known representative, *P. rubrum*, causes a red spot disease of *Prunus domestica*, *P. insititia* and *P. spinosa* (Blackman and Welsford, 1912; Nienburg, 1914). The ascospores germinating in the spring infect the young leaves bursting from the buds and grow to a large intercellular mycelia. The hyphal cells are uni- to trinucleate and contain an orange-yellow, alcohol-soluble pigment; their walls are at first thin, later becoming thick and gelatinous. In 5 or 6 weeks they fill the whole space between the epidermal layers and during the summer form shining, reddish yellow or scarlet sclerotic stromata.

Before this development has proceeded far, flask-shaped pycnidia are formed from knots of unthickened hyphae under the stromata.

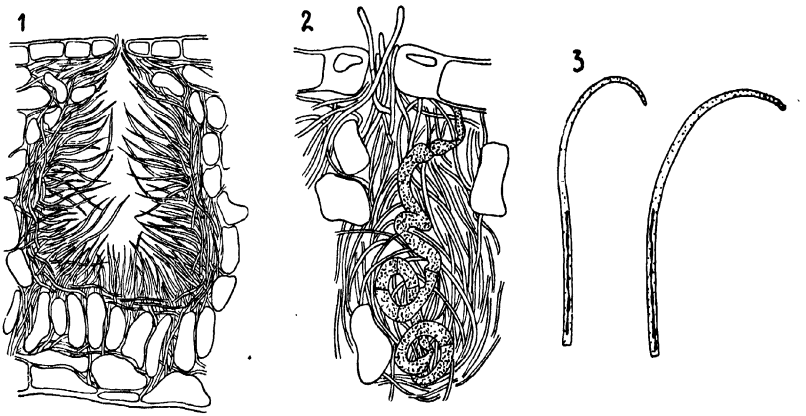


FIG. 147.—*Polystigma rubrum*. 1. Section through portion of leaf with young pycnium. 2. Section through young perithecial fundament showing helical ascogonium. 3. Pycnospores. (1 × 200; 2 × 600; 3 × 1,200; *after Blackman and Welsford*, 1912.)

The pycnidial wall consists of a plectenchyma from which the sporiferous hyphal branches radiate (Fig. 147, 1). The pycnospores are terminal, uninucleate, tapering upward and falcate at their tips (Fig. 147, 3). They are embedded in a slimy substance and in damp weather are forced out of the mouth of the pycnia upon the leaf.

Later, in July or August, the perithecium is formed, as a small hyphal tangle in which is embedded a helical ascogonium (Fig. 147, 2). Its development is incompletely known; a half schematic cross section of an older stage is shown in Fig. 148, 1. The basal cell of the ascogonium bordering on the ascogonial hypha is short and has few nuclei. Adjacent to it is an elongated cell with many small nuclei. The next cell has only a single, rather large nucleus but is much shorter than both the previous ones. There follow two cells with two small nuclei each; then the helix continues with cells with an irregular number of nuclei and finally is lost

in vegetative tissue. There regularly appear, however, always in the same order, the long cell with many small nuclei, the long cell with one large, and the short cell with one large nucleus. At this time the trichogyne is not present. Later, however, some ascogonial cells develop to longer, occasionally branched, hyphae which, like the remaining

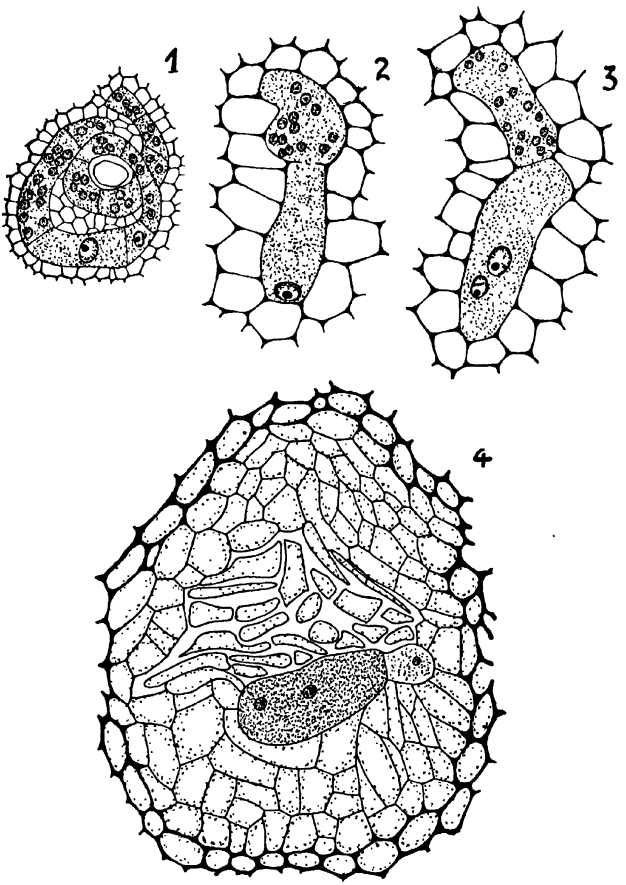


FIG. 148.—*Polystigma rubrum.* 1. Young ascogonium showing all essential parts except the trichogyne. 2. Wall between two ascogonial cells partially resorbed. 3. Completed plasmogamy. 4. Beginning of perithecial formation. Only the dicaryotic cell of the ascogonium remains. (× 860; *after Nienburg*, 1914.)

hyphae, stretch toward the stomata but seldom reach the surface (Figs. 147, 2; 149, 1 to 3). They are called trichogynes by the authors cited here.

The development of the ascogonium at first proceeds very slowly and fertilization takes place only in December in the dead leaves lying on the

ground. Between the long, multinucleate, male and the long, uninucleate, female cell, there is formed a pore (Fig, 148, 2) and one of the many male nuclei migrates into the female cell. Then the pore is closed (Fig. 148, 3) and the nuclei remaining in the male cell gradually degenerate.

Not only the ascogonium but also the surrounding vegetative cells show an increased vitality, probably because of stimulation of the sexual act. They begin to change to rafter-like, super-imposed paraphyses, while the ascogonium dies, except for the single cell with its dicaryon.

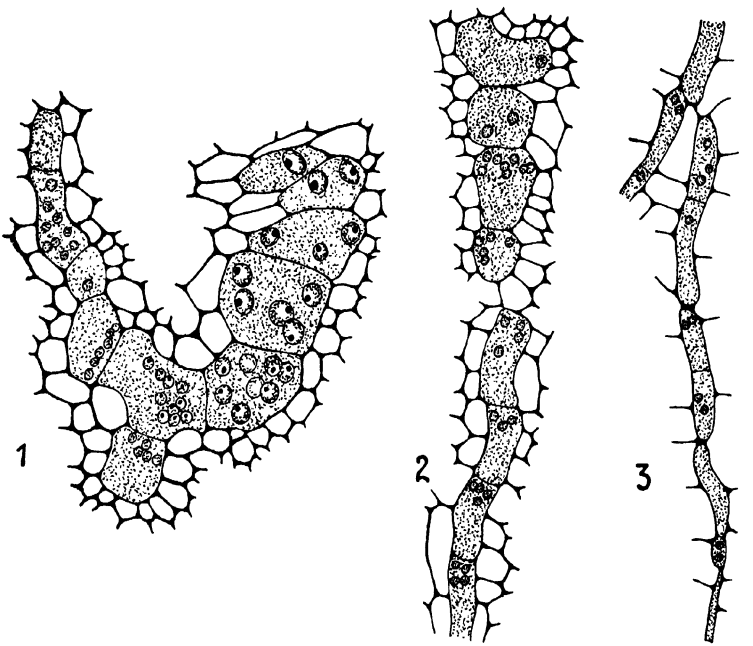


FIG. 149.—*Polystigma rubrum*. 1. Part of mature ascogonium from which trichogynes extend to the left above and below. 2. Continuation of lower left trichogyne of 1. 3. Further continuation of the trichogyne of 2. (Note the renewed branching.) (× 860; *after Nienburg*, 1914.)

By forcing aside these paraphyses, the perithecial cavity, filled by paraphyses, is formed. During January the ascogenous hyphae grow into the cavity and change to asci. In March the development of the ascospores is completed.

This life cycle of *Polystigma rubrum* is generally interpreted according to the relations of the lichens to be discussed later in the Discomycetes, that the pycnia are spermogonia, and the structures here designated as pycniospores (and they are certainly very difficult to germinate) as functionless spermatia which earlier may have fertilized the ascogonia.

Thus also, the ascogonium would be designated as a rudimentary trichogyne. *P. rubrum,* thus, would be considered a form in which spermatial fertilization was lost and replaced by a parthenogamous sexual act.

It must be emphasized, however, that among these proposed ideas there is no place for spermatial fertilization. The numerous examples of development of Hypocraeales and Sphaeriales are adapted without exception and with astonishing uniformity to the scheme of the Plectascales, hence the Pyrenomycetes undoubtedly have arisen from the Plectascales type. Thus there is no phylogenetic necessity for assuming prehistoric spermatial fertilization and, besides, such a fertilization would be practically impossible, for the pycnia (spermatogonia) develop in spring or early summer and then disappear. The ascogonia which they should fertilize arise months later on the same stroma; spermatial fertilization, seems improbable. The fact that we know insufficiently the conditions for the germination of these pycniospores is not proof that they are functionless spermatia. Brefeld, Tavel and Möller (not using single spore cultures or probably even pure cultures!) have reported germination of microconidia with mycelial development. The function of microconidia needs furthur study.

It seems much more important for the explanation of relationships of *Polystigma,* to refer to its saprophytic, more easily investigated relatives such as *Melanospora* and the Aspergillaceae, whose imperfect forms do not resemble these and germinate easily, hence scarcely have the significance of disguised spermatia. In *Melanospora parasitica, M. Zobelii,* etc., as in the typical Aspergillaceae, are still formed two copulation branches which, at least in *M. Zobelii,* occasionally come into open communication at the tip. In other forms, only the helical ascogonium is formed, from which alone, development proceeds. Gäumann prefers to consider *Polystigma rubrum* as a reduced form of this type in which (and here is the fundamental significance) in spite of the degeneration and disappearance of the antheridium, caryogamy is still necessary, but leads to parthenogamy within the ascogonium. Thus the loss of the original cross fertilization is compensated. Unfortunately the reduced species of the Aspergillaceae and *Melanospora* corresponding to the *Polystigma* type have been insufficiently investigated, hence we are too uncertain whether the binucleate condition which leads to the formation of ascogenous hyphae, is caused by a usual nuclear pairing in any cells, or by a parthenogamy as in *Polystigma.* If forms which belong to the last type are discovered, the interpretation of *Polystigma* given here would be much reinforced.

Concerning the nature of the ascogonial processes called rudimentary trichogynes, we can only offer conjectures. It is possible that these structures correspond to true trichogynes; but it must be emphasized that this in no way involves a spermatial fertilization, for the simplest

ancestral form of basidia. In good nourishment the conidiophores branch and form coremia.

Some species are used as food, *e.g.*, *Polyporus confluens*, *P. frondosus*, *P. pes-caprae* and *P. sulphureus;* earlier, others were used as medicines (*Fomes officinalis* from its quinine taste); others found technical uses, as *P. betulinus* in the manufacture of charcoal crayons. Still others cause disease of fruit and forest trees and destroy timber, as *Fomes igniarius*, *F. fomentarius*, from whose fructifications tinder was formerly made, *Polyporus squamosus* and *P. sulphureus* and, on old gooseberries and currants, *Fomes Ribis*.

The fructifications of *Fomes igniarius* grow to as much as eighty years old forming a new layer each year. A few species of *Polyporus* form sclerotia up to the size of a human head, as *P. Tuberaster* (E. Fischer, 1891) in the north temperate zone, *P. Berkeleyi*, *P. umbellatus* and *P. frondosus* in the United States, *P. sacer* and *P. Goetzii* in Africa, *P. Sapurema* in Brazil, *P. rhinocerotis* in the Malay region and *P. basilapidiodes* and *P. Mylittae* in Australia. Those of *P. Mylittae* attain a weight of 15 kg. and earlier were eaten by the natives in Australia and called native bread.

The species of *Polystictus*, which number almost a thousand, are saprophytes on wood. *P. versicolor* often attacks fruit trees as a wound parasite. *P. pargamenus* causes decay of a large number of woods.



FIG. 288.—*Trametes* species on wood. Lower view of bracket fructifications showing *Daedalea*-like elevations of hymenophore. (Natural size; *after Falck*, 1909.)

Trametes, as its character is not always recognizable, has been divided by many authors among the above three genera and *Daedalea* (Fig. 288). *Trametes Pini* causes great damage to pines by a red rot of wood. Under certain conditions of nourishment, their hyphae (as in most other Polyporaceae) fall apart into oidia.

Hyaline, pyriform or oval conidia have been noted in *Cryptoporus volvatus* (Zeller, 1915). The hymenium develops on the roof of a large central cavity opened in the interior of a spherical fructification, laterally attached to the substrate. Gradually the portion below the hymenium ceases to grow, the hyphae are stretched into a thinner layer and a small central opening is formed in the veil ("volva"). The spores are shed upon the upper side of the veil, whence they are dispersed by clinging to the legs of insects which crawl over it. The development is therefore hemiangiocarpous, the only case known in the Polyporales and the only group in this order which depends on insects for spore dissemination.

Gemmae and conidia are known as imperfect forms. The gemmae are mostly hyaline or brownish and occasionally verrucose; they develop (especially in drying cultures) on hyphae, singly or catenulately, and

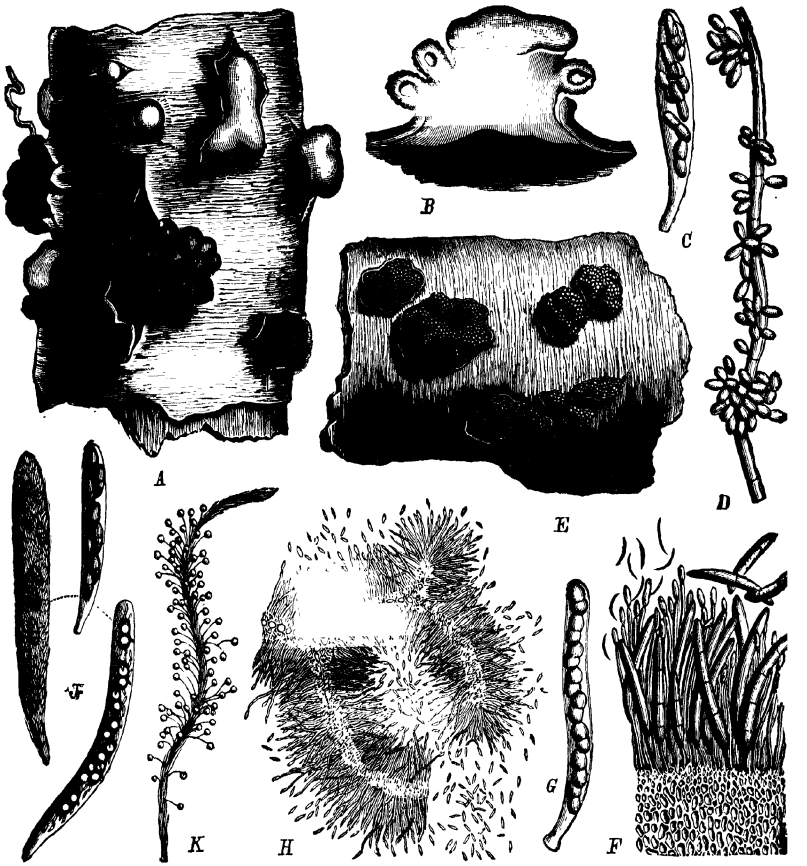


FIG. 150.—*Nectria cinnabarina*. *A*. Conidial stromata (shown light) perithecial stromata (dark) erumpent from bark of host. *B*. Section through a stroma which is still cutting off conidia at the top while it has formed perithecia on the sides. *C*. Ascus. *D*. Hypha with microconidia. *Nectria ditissima*. *E*. Perithecial layer breaking from the bark. *F*. Longitudinal section of conidial fructification. *Nectria sinopica*. *G*. Ascus. *H*. Part of pycnium. *Nectria inaurata*. *J*. Ascus without and with sprout cells. *Nectria oropensoides*. *K*. Coremium. (*A* × 10; *B* × 20; *C*, *D*, *G*, *J* × 350; *E* × 3; *F*, *H* × 380; *K* × 60; *after Tulasne, Brefeld and Lindau.*)

show little individuality. The conidia, also in exhausted nutrient solutions, may thicken their walls and change into a sort of gemmae.

The conidia are hyaline or yellowish, brownish, orange red, etc., and are cut off, either terminally or laterally, from hyphae which are

differentiated to special, more or less developed conidiophores. Often they are embedded in slimy masses which are called **pionotes.** In *Nectria oropensoides* and *N. Peziza*, the conidia adhere to the conidiophores in small slimy heads; in luxuriant cultures, the conidiophores unite to coremia surrounded by capitate spore masses (Fig. 150, *K*). Under certain cultural conditions, the conidiophores change to flat, pulvinate stromata, or sporodochia (Fig. 150, *F*); these suggest, morphologically, horizontally broadened coremia and often consist of thick-walled, plectenchymatic stromata and conidiophores radiating from them.

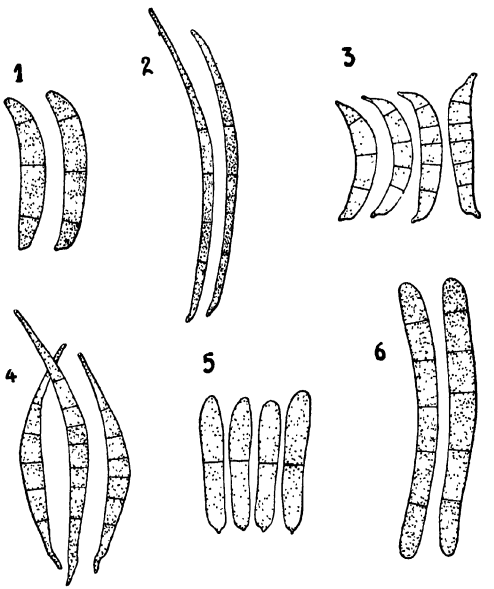


FIG. 151.—Conidial types of the *Fusarium* group. 1. *F. Solani.* 2. *F. subulatum.* 3. *F. discolor.* 4. *F. gibbosum.* 5. *F. didymum.* 6. *F. Willkomii.* (× 670; *after Appel and Wollenweber*, 1913.)

In *Nectria* and *Pleonectria*, these sporodochia develop to pulvinate or gibbous fructifications often of characteristic form (Fig. 150, A and B); these imperfect forms were formerly classified in the genus *Tubercularia* of the Fungi Imperfecti. Exceptionally, the conidiophores are formed in the interior of irregular winding cavities (Fig. 150, *H*) instead of superficially; thus, in *Nectria sinopica* on hard stems of ivy, the orange-red mycelium, with suitable food, collects in knots which in about two months are differentiated to pycnia and at maturity forces white coils of very small, hyaline conidia from the ostioles.

For practical purposes, the conidia may be divided into macro- and microconidia; both types are only the two extremes of the same

spore form and connected with each other by transitional forms; still, often depending on conditions, one or the other type predominates. The microconidia are small, spherical or elongate and 1 to 2 celled (Fig. 150, *D*); they were earlier placed in the Imperfect genus *Cephalosporium*, as they are collected into small heads. The macroconidia are larger and often falcate; on account of this shape they were placed in the Imperfect genus *Fusarium* along with the conidia of many other Hypocreales. They are mostly multiseptate, but under unfavorable conditions of growth the septa may be subsequently dissolved or they may never be formed. For the purpose of easier survey, these *Fusaria* important in plant pathology have been grouped, according to form, size and septation, into several types, as *F. Solani*, *F. subulatum*, *F. discolor*, *F. gibbosum*, *F. Willkommii* and *F. didymum* (Fig. 151).

The fructifications of the perfect form, the perithecia, arise generally singly or in loose groups and rest loosely on the substrate or on a more or less strongly developed subiculum (Fig. 151, *B*). In the forms with *Tubercularia* stromata, they are laid down on or in these stromata (Fig. 152, *B*) and are then generally united in groups; they may often be found singly, however, also on the same piece of bark, without stromatal development. Their formation is preceded by the formation of a helical ascogonium whose cells are multinucleate in the species so far studied, *Nectria Ribis*, *N. galligena* and possibly *N. Ipomoeae* (Vincens, 1917; Cayley, 1921; Cook, 1923); unfortunately more details of cytological development are unknown. The perithecial rind is generally deeply colored: in *Nectria*, *Calonectria* and *Pleonectria*, yellow, red or brown, in age often almost black; in *Gibberella* brown or violet. Here also as in the mycelial mats, however, the colors are frequently dependent on the reaction of the substrate; thus the perithecia of *G. Saubinetii* are blue on alkaline media, red to brown on acid.

Systematically these four genera have, if possible, a larger variety of forms than the *Aspergillus–Penicillium* group of the Plectascales, and hence, up to the present, have defied satisfactory solution (Appel and Wollenweber, 1914). There is no doubt that in the principles of division employed at present (of the forms with yellow or red perithecia, the Didymosporae to *Nectria*, the Phragmosporae to *Calonectria*, the Dictyosporae to *Pleonectria*, and of the forms with violet or blue perithecia, the Phragmosporae to *Gibberella*), species from entirely different developmental series, on the basis of these two chosen characters, are placed together in artificial heterogenous genera; up to the present, however, these principles cannot be replaced by a better artificial or phylogenetic system. Theissen (1911) attempts for *Nectria* to utilize the condition of the ascospore membrane (smooth spores to the Leiosporae, longitudinally striate spores to the Rhabdosporae and verrucose spores to the Cosmosporae). Wollenweber (1924) attempts to utilize the imperfect

forms. Weese (1914, *et seq.*) attempts to create developmental series according to the structure of the perithecial wall. Consequently the different genera are differently defined by different authors; all these attempts, however, have not yet afforded a complete system.

The most important plant pathogens in the genus are: *Nectria cinnabarina*, a wound parasite in most of our frondose trees and shrubs, causing canker and dieback of the twigs and forming on the dead twigs striking red conidial fructifications, *Tubercularia vulgaris* (Fig. 152, *A*, *D*); *N. cucurbitula*, a wound parasite of conifers; and *N. galligena*, the European canker of apple (imperfect form, *Cylindrocarpon* [*Fusarium*] *mali*). Often the harmless saprophytic *N. ditissima* (imperfect form *Cylindrocarpon* (*Fusarium*) *candidum*), which is only pathogenic for beeches, on account of its association with *N. galligena*, is often considered as the cause of the canker. In *Calonectria*, *C. graminicola* (*C. nivalis*, *Fusarium*

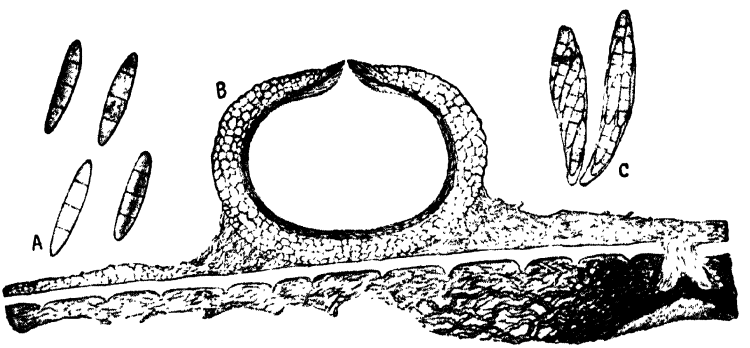


FIG. 152.—*Calonectria crubescens*. *A*. Ascospores (× 750). *B*. Mature perithecium with subiculum (× 140). *C*. Mature asci (× 400). (*After Weese*, 1914.)

nivale), the "snow mould" chiefly on rye, causes a wad-like covering and death of seedlings; furthermore in damp summers it appears at the base of the stems and causes a foot rot of grain (Schaffnit, 1912, 1913). *Gibberella Saubinetii* (*Botryosphaeria Saubinetii* according to the nomenclature of Weese 1919) causes foot disease and scab of small grains; *Pleonectria berolinensis* causes the death of *Ribes*.

Hypomyces differs from the four previous genera in the extensive development of gemmae. It is chiefly parasitic on agarics and forms a stroma on the underside. The infection is generally visible by the appearance of a fine, arachnoid mycelium whose hyphae cut off acrogenously fine, hyaline, generally unicellular conidia; in this stage, the fungi in question have been assigned to various imperfect genera, as *Verticillium*, *Botrytis* and *Sporotrichum*. Later there appear on the same hyphae, thick-walled, often sulptured gemmae. These two forms were earlier regarded as independent species and assigned to *Sepedonium*, *Mycogone*,

etc. *Hypomyces ochraceus* on *Russula* has hyaline conidia, called *Verticillium agaricinum*, its ochraceous gemmae being *Mycogone puccinioides*. *H. chrysospermus* lives mainly on *Boletus;* its golden-yellow gemmae were called *Sepedonium chrysospermum*. The imperfect *Mycogone rosea*, which also may belong to *Hypomyces*, along with others lays waste the mushroom cellars. *Hypomyces* species, whose conidia are of the *Thielavia* type, are placed in *Pyxidiophora*. As far as the cytological development is known for *Hypomyces*, it follows the *Melanospora* type. In *H. rosellus* (Dangeard, 1907) and *H. aurantius* (Vincens, 1917), the hyphal cells are multinucleate, in *H. ochraceus* (Dangeard, 1907) uninucleate.

The representative of the second stage in which the perithecia are united on or in undifferentiated stromata, as *Sphaerostilbe* in the Didymo-

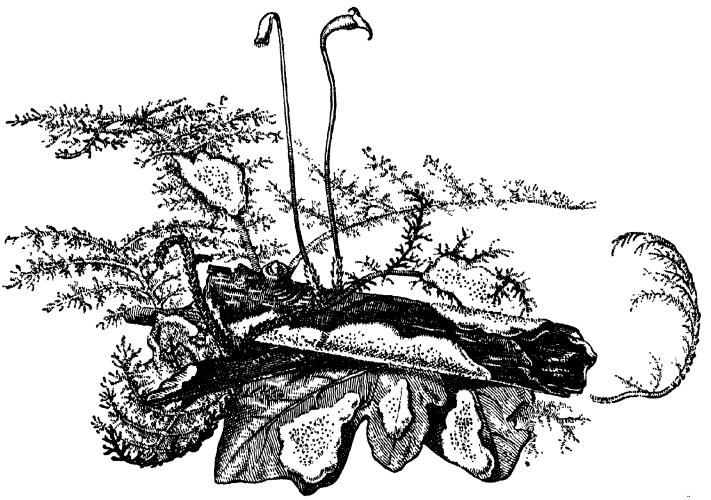


FIG. 153.—*Hypocrea delicatula*. Habit. (Natural size; *after Tulasne.*)

sporeae, *Stilbonectria* in the Phragmosporae, and *Megalonectria* in the Dictyosporae, arise directly from the stromatic forms of the first stage and frequently may not be easily distinguished from them. Their conidiophores, in contrast to the stromatic Nectriaceae, are joined into clavate coremia at whose base the perithecia develop. In the Brazilian *Megalonectria verrucosa*, the ascospores germinate to a sprout mycelium in the interior of the ascus, as in some Nectriaceae. *Sphaerostilbe repens* causes a root disease of *Hevea* in Ceylon.

In the representatives of the third stage, the stromata gradually develop to definitely formed fructifications; they have been studied in five genera: *Hypocrea, Corallomyces, Mycocitrus, Peloronectria* and *Shiraia*. The species of *Hypocrea* are distinguished in that their bicellular ascospores at maturity separate into single cells, so that the asci apparently

contain sixteen spores. Their lowest representative connects directly to the *Melanospora–Nectria* type. Thus in *H. delicatula,* the perithecia stand comparatively irregularly on or in a slightly developed stroma (Fig. 153). In other forms, the stromata have an even greater development; thus, in the cosmopolitan *H. citrina,* they appear in the form of irregularly formed, yellow or ochraceous, thin mats on earth, leaves or tree trunks, often flat, up to one-half meter in cross-section.

In the higher species, the stromata no longer form irregular crusts growing indefinitely in all directions, but begin to be individualized: they attain definite outlines and become fructifications. A first stage is represented by *H. rufa,* whose stromata are still rather indefinitely formed and spread over the substrate as flesh-colored, later red-brown,

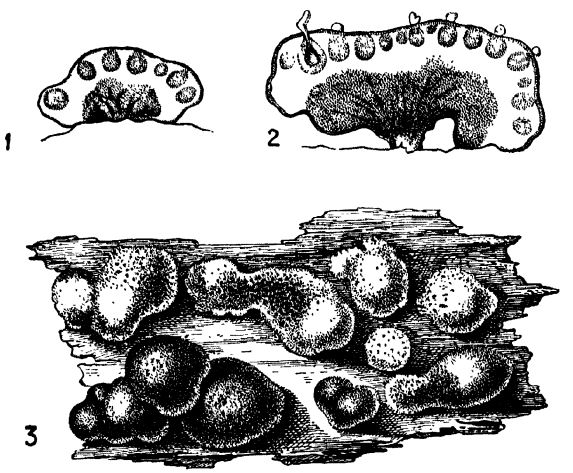


FIG. 154.—*Hypocrea rufa.* 1, 2. Sections through poorly and well-developed specimens. 3. Habit. (Natural size; *after Tulasne.*)

often confluent cushions (Fig. 154, 3). Under favorable conditions of nourishment they are raised from the substrate by slight stipes and then become differentiated into sterile portions directed toward the substrate, and fertile portions directed away (Fig. 154, 2). The conidia of this species cover the cultures with a greenish powder (*Trichoderma viride*). They show a change in color similar to that of the conidia of numerous other Hypocreales changing from greenish on acid to yellow on alkaline media (Milburn, 1904).

In a closely related segregate, *Hypocreopsis lichenoides* (*Hypocrea parmelioides, Hypocreopsis riccioidea*) and *H. Rhododendri,* the stroma develops centrifugally into thick, subdichotomous lobes, resembling *Parmelia physodes.* The perithecia are confined to the upper, outer surface and are progressively developed as the lobes extend outward (Thaxter, 1922).

Somewhat higher is the Brazilian, *Hypocrea pezizoidea* forming cup-shaped pezizoid fructifications in whose interior are embedded the perthecia. Higher still is *H. poronioidea* in which the stromata, as in the agarics, are differentiated into a stipe and pileus and on whose upper surface are embedded the perithecia.

Highest of all are *Podostroma alutacea* and *P. cornu-damae*. *P. alutacea* grows through the whole north temperate zone, forming a vertical clavate fructification (up to 3 cm. high), which divides into a sterile stipe and a narow clavate head (Fig. 155, 1). Externally it appears like *Xylaria* of the Sphaeriales or *Clavaria* of the Basidiomycetes (Atkinson, 1905). In the Thibetan *P. cornu-damae*, the 10-cm. high fructifications are branched like a staghorn and appear deceptively like the Clavariaceae.

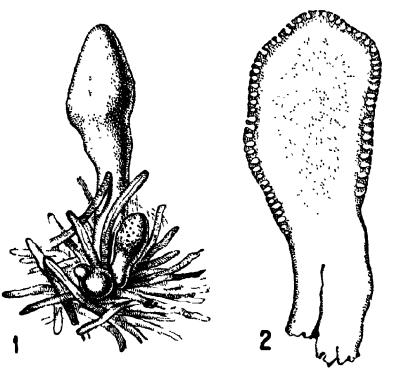


FIG. 155.—*Hypocrea alutacea*. Habit and section through a fructification. (Natural size; *after Tulasne.*)

In another direction has developed the genus, also belonging to the Didymosporae, *Corallomyces*, whose best-known representative, *C. Jatrophae*, is parasitic in Brazil on *Aipim* (*Manihot, Jatropha Aipi*). Its fructifications are rarely more than 3 mm. high and are differentiated into a pure white, flat, at times patelliform disc and into a red stipe fading towards the top (Fig. 156, 1 and 2). On this disc are at first cut off an enormous number of hyaline, falcate *Fusarium* conidia held by a watery excretion in the form of a milk-white drop (Fig. 156, 4); with the slightest shaking the drop flows off but another is formed in the course of a few hours. At times the edges of the disc grow further towards the sides in irregular folds; thereby arise flat, ruffled covers (Fig. 156, 5), which may attain a cross section up to 1 cm. and (as in *Hypocrea rufa*) hide the stipe. Under certain conditions of nourishment, the conidia may arise not only on those patelliform fructifications, but also on the top of coralloid, bright red, sclerotic structures which have given the genus

its name (Fig. 156, 3). When conidial formation is exhausted, the small, dark red perithecia, about 1 mm. high, with a conical ostiole arise beneath the drop of slime that crowns the typical fructification. This genus connects directly with the stromatic Nectriaceae; it has in common with them the development of a succession of conidia and perithecia on the same stroma, and differs from them only in the more highly differentiated structure of its stromata.

Towards a third direction has developed the *Mycocitrus–Shiraia* group, of which we discuss *Mycocitrus* under the Didymosporae, *Peleronectria* under the Phragmosporae and *Shiraia* under the Dictyosporae. All three are epiphytic on bamboo twigs. In Brazil, *Mycocitrus aurantium* forms a golden-yellow fructification, up to 12 cm. in cross section,

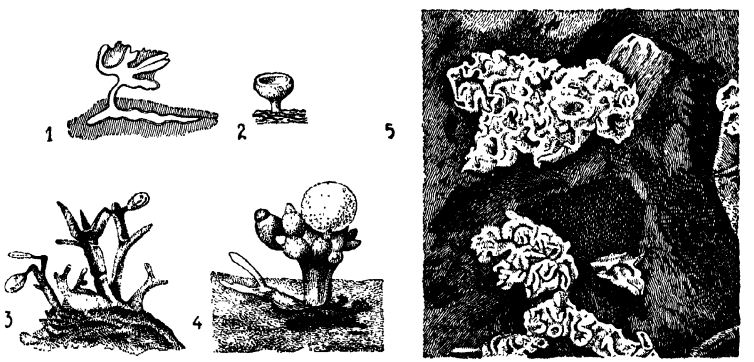


FIG. 156.—*Corallomyces Iatrophae.* 1. Longitudinal section. 2. Conidial fructification. 3. Coralloid conidial fructification. 4. Young perithecia and conidial gel. 5. Hypogaeous conidial fructifications on *Aipim* roots. (1, 2 × 3; 3, 4 × 4; 5 × 1½; *after Möller*, 1901.)

which, as its name indicates, looks like an orange (Fig. 157). The context consists of a light-colored, glassy mass which is permeated by darker veins consisting of thick-walled hyphae. The perithecia are formed in the rind over the whole surface of the fructification and form a large number of spores; Möller (1901) reckons them at over a billion per fructification. When a perithecial generation is exhausted and emptied, it becomes overgrown by a stroma which forms a new perithecial layer, suggesting conditions in certain perennial Basidiomycetes.

Peloronectria vinosa, also Brazilian, forms irregular, soot-gray to brown-yellow lumps which do not bear the perithecia on their rind but raised above the fructification on short columnar outgrowths. The conidial form, which appears in artificial cultures, corresponds to the *Fusarium* type, as in *Mycocitrus aurantium.* The Japanese *Shiraia bambusicola*, finally, corresponds to *Mycocitrus* of the Dictyosporae and

forms lumps 2 to 3 cm. in diameter, in whose periphery are embedded the perithecia (Hennings, 1901).

The second group of the Hypocreales, that of the Didymosporae–Phragmosporae–Dictyosporae, shows morphologically the same fundamental characters as the first group, the Amerosporae. It begins with simple forms without stromata and develops gradually to a continually more differentiated stromatic type which reaches a height of development in each of three spore series corresponding to that of the lower Polyporales of the Basidiomycetes. While these four series in the table on page 233 follow rather identical lines in the differentiation of their stroma and hence end with fructifications externally alike, in the third group of the Hypocreales, that of the Scolecosporae, we will have to follow at least three divergent directions of development: the first, represented by the *Oomyces–Ascopolyporus* series, which reaches the height of the Polyporales in the formation and structure of a perithecial hymenium; a second represented by the *Epichloe–Claviceps* series which, by physiological differentiation of its stromata, has arrived at types peculiar to the Hypocreales; and a third, represented by the *Cordyceps* group, which is a copy of *Hypocrea* and its relatives in the Didymosporae.

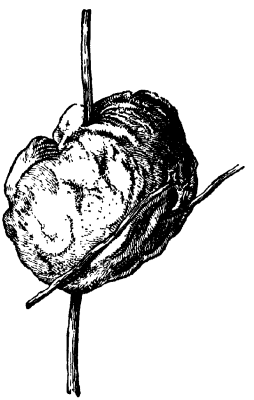


FIG. 157.—*Mycocitrus aurantium*. Perithecial stroma. (Natural size; *after Möller*, 1901.)

The *Oomyces–Ascopolyporus* series, through *Oomyces*, is connected directly to the level of the stromatic Nectriaceae. *Oomyces* forms flattened, slightly differentiated mats in which are embedded the perithecia. In Brazil *Oomyces monocarpus* develops on *Merostachys speciosa*, a bamboo, small, soft, light yellow to reddish stromata, 1 to 2 mm. high, each of which contains a single perithecium. Occasionally several stromata may be confluent at the base or may come together into small mats. The structure of the perithecial wall is markedly different from the structure of the stroma. Still more marked is this differentiation in the Javan *Oomyces javanicus*, forming its stromata on the undersides of the leaves of *Vaccinium varingifolium*. Here the differentiation between perithecium and stroma has gone so far that pressure on the cover glass easily forces the perithecium out of the stroma.

In *Konradia* and *Hypocrella*, the stromata begin, as in the *Sphaerostilbe–Megalonectria* group of the Didymosporae–Dictyosporae, to individualize and develop to fructifications of definite form. On bamboo twigs in Java, *Konradia bambusina* forms irregular lumps, on whose upper surface are imbedded the perithecia. While the outer parts with the older perithecia die, become carbonaceous and crumble, intercalary

growth continues at the base, forming new perithecia in the new growth zones. Thus the fructifications may attain a cross section of several centimeters.

The species of *Hypocrella* are also epiphytic or ectoparasitic on stems and leaves. The Brazilian *H. cavernosa* corresponds in the essentials of its form to *Konradia bambusina*. On *Merostachys speciosa*, it forms spherical stromata on which *Fusarium* conidia are cut off in depressions and labyrinthine cavities and later form perithecia. In the Brazilian *H. verruculosa*, on bamboo, the surface of the stroma begins to be differentiated in a characteristic manner. After a time, the stroma grows on a limited circular spot which develops a reticulate system of channels. In the Brazilian *H. Gaertneriana*, on bamboo, these protrusions develop to verrucose protuberances on which alone the perithecia are formed (Fig.

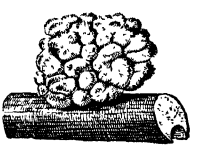


FIG. 158.—*Hypocrella Gaertneriana* on bamboo. (Natural size; *after Möller*, 1901.)

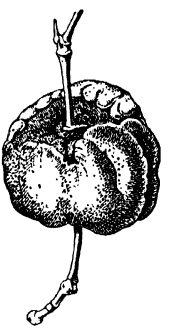


FIG. 159.—*Mycomalus bambusinus* on bamboo. (Natural size; *after Möller*, 1901.)

158). In this species the surface of the stroma, for the first time in the Scolecosporae (as in *Xylocrea* of the Amerosporae) is differentiated into a fertile and a sterile part.

This division of the surface of the fructification into fertile and sterile zones extends still further in the following genera on bamboo, in a characteristic manner on each: in *Mycomalus* leading to the formation of a single equatorial fertile ring and in *Ascopolyporus* to dorsiventral brackets. In Brazil on dead twigs of *Guadua taguara* (even on those 2 mm. in diameter), *Mycomalus bambusinus* forms chestnut brown, apple-shaped balls up to 5 cm. in size, around which extends the pulvinate, melleous, fertile zone as a broad girdle arching over above and below (Fig. 159). Its perithecia are very far apart, only about 9 per square centimeter.

In *Ascopolyporus*, differentiation is more horizontal. In the lower forms, as *A. polychrous* and *A. villosus*, the fructifications are still spherical; in the latter, however, the upper side of the sphere is distinguished from the lower by a tomentum visible to the naked eye. In the highest known member of the genus, *A. polyporoides*, the fructifications are flat-

tened (Fig. 160); its upper side is covered by a solid rind while the lower only form the perithecia. In this form, the Hypocreales have a type of fructification which one would, without study, consider polyporaceous. In *Ascopolyporus*, the imperfect forms are Fusaria, while in *Mycomalus* they are reminiscent of *Ustilaginoidea*.

The second series of the Scolecosporeae, *Epichloe–Claviceps*, is epiphytic or parasitic on Gramineae. *Epichloe* possesses flat undifferentiated stromata which correspond to the lower species of *Hypocrella*. *E. typhina* forms sheaths around the stems of the meadow grasses; the young stromata form enormous numbers of small, hyaline conidia; later they develop the golden-yellow perithecia, at first singly, later in a continuous layer. *E. bambusae*, in the Sunda Archipelago, infects several species of bamboo, *Gigantochloa apus*, *Dendrocalamus flagellifer* and *Bambusa Blumeana*, and stimulates them to the formation of long, pendant witches' brooms. Unlike *E. typhina* it possesses no imperfect forms. The ascogonium consists of a row of two to five cells, each containing three to seven nuclei. The wall between two cells disappears and the nuclei pair. The details of the process are not clear but the ascogenous hyphae grow from these cells, eventually producing asci as in *Pyronema confluens* (Gäumann, 1927).

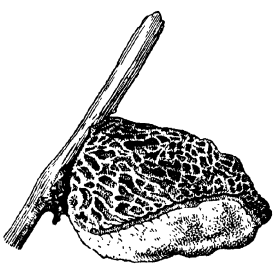


FIG. 160. — *Ascopolyporus polyporoides* on bamboo. (Natural size; *after Möller*, 1901.)

While in *Epichloe typhina* the fundaments of the perithecia are limited to irregularly defined spots and, by the confluence of the perithecia, develop into a homogeneous stroma, in *Ophiodotis*, they are retained to the maturity of the stroma; as in the higher species of *Hypocrella*, *Mycomalus* and *Ascopolyporus* the upper surface of the stroma is differentiated into fertile and sterile zones.

The Brazilian *Ophiodotis Henningsiana* on *Andropogon*, forms black stromata several centimeters long, resembling those of *Epichloe*. At the time of perithecial formation the thin stroma thickens in spots, often as much as fivefold, so that at maturity the fungus forms an uneven, verrucose stroma (Fig. 161, 2). On account of this dark color and the fragility of the stromata, *Ophiodotis* is usually placed in the Sphaeriales; but its transfer to the Hypocreales, where it doubtless belongs in the *Epichloe–Claviceps* series, is desirable since many Xylariaceae are only slightly harder than many species of Hypocrella.

The South American *O. raphidospora* keeps the perithecial thickening within more definite limits. It appears on young, still rolled, bamboo leaves in the form of black stripes several centimeters long and hinders the unfolding. As in *Epichloe Bambusae* the plectenchyma completely fills the spaces between the leaves and transforms them to pseudomorphs.

The stroma thickens under the outer layer of leaf, and ruptures it lengthwise in stripes or welts (Fig. 161, 3). The perithecia are formed in two parallel rows in these cushions.

In *Balansia* morphological differentiation of the stroma is more marked since the plectenchyma which surrounds the host becomes more scle-

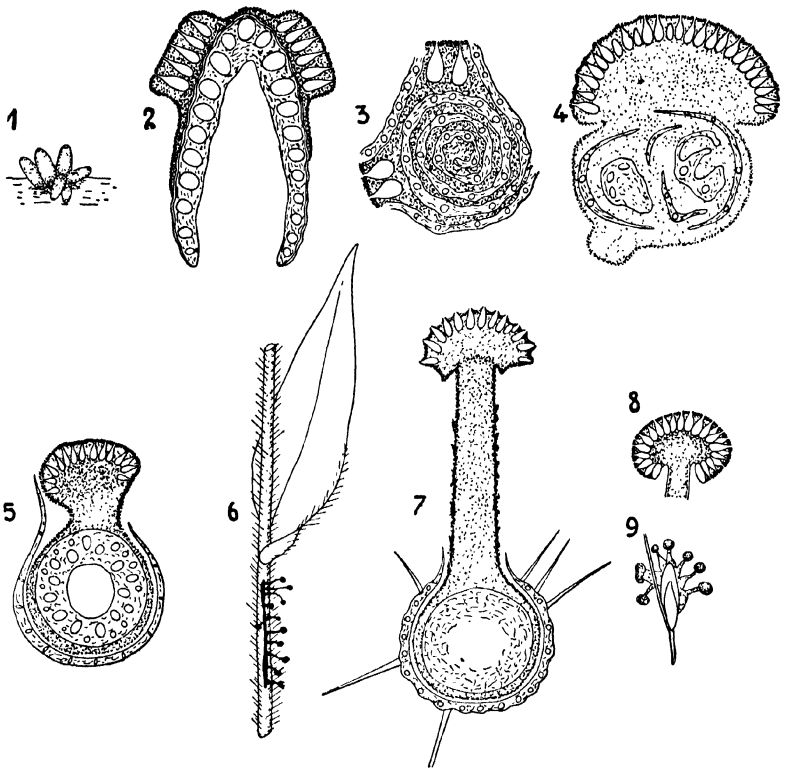


FIG. 161.—1. *Oomyces monocarpus*. Group of fructifications on bamboo twig. 2. *Ophiodotis Henningsiana*. Section through an infected leaf. 3. *Ophiodotis raphidospora*. Section through a rolled leaf showing stroma. 4. *Balansia Hypoxylon*. Section of pseudosclerotium and mature stroma with perithecia. 5. *Balansia ambiens*. Section of grass stem with perithecial stroma. 6, 7. *Balansia redundans*. Habit, and section through stem and stroma. 8, 9. *Balansia diadema*. Section of stroma and infected spikelet of *Panicum* with fructifications. (1 × 3; 2, 5 × 13; 3, 4 × 4; 6, 9 natural size; 7 × 10; 8 × 7; *after Atkinson*, 1905, *and Möller*, 1901.)

rotic in age and perithecial formation takes place on special prosenchymatic outgrowths which break through the hard stroma. The simplest forms, as *Balansia Hypoxylon*, are directly connected to *Ophiodotis raphidospora*. In the Southern states, *B. Hypoxylon* is parasitic on various grasses and surrounds the stems with a plectenchyma, fleshy when young, sclerotic in

age. At a definite time this develops to a linear stroma which is only slightly raised from the dark sclerotium (Fig. 161, 4).

In the Brazilian *B. ambiens*, the perithecial outgrowths are more sharply separated from the pseudoparenchymatous stroma. *B. ambiens* on the stems of *Olyra* emerges between the leaf sheaths in the forms of a linear stroma 1 mm. broad. The stroma is hard and remains sterile; in solitary irregularly scattered spots, it develops to a short stipitate black heads about 2 mm. thick in which the perithecia are formed (Fig. 161, 5).

In a third species, *B. redundans*, this little head projects above the sclerotic plectenchyma on a stipe 5 mm. long (Fig. 161, 6 and 7). Thus the fertile tissue has attained a definite form while the sterile tissue still has a formless stromatic texture.

A fourth species, *B. diadema*, is important for the course of our dicussion, in that it does not parasitize the stems but rather the reproductive organs of the grasses. It surrounds one or two spikelets of a Brazilian *Panicum* with a comparatively soft stroma whose exterior is darker but not differentiated as a true rind; a thickly interwined hyphal tissue protruding between the glumes, replaces the pistil (Fig. 161, 9). The perithecial heads sprout from this dark stroma, as in *B. ambiens* (Fig. 161, 8). In a fifth species finally, *B. Claviceps*, widely dispersed in the tropics on *Setaria* and *Penisetum*, the spikelets are surrounded, as in *Balansia diadema* (Fig. 162, *A*) but, in contrast to that species, the stromata are sclerotic as in those of *B. ambiens*.

Claviceps forms the end of this series in which the stromata develop to true sclerotia with thick rinds, suited for long resting periods. The separation of the stroma into fertile and sterile parts, lacking in *Epichloe*, barely indicated in *Ophiodotis*, and leading to a definite form of the fertile part in *Balansia*, is still sharper in *Claviceps;* each of the two parts has its characteristic form and develops as its special function requires.

The simpler species of *Claviceps*, as the Brazilian *C. balansioides*, connect directly to *Balansia Claviceps*. *C. balansioides* also entangle the flowers and floral organs of grasses (*Echinochloa* sp.), surrounding the whole tangle with a sclerotic stroma. The enclosed floral organs are retained largely, and the sclerotia are only plumper reproductions of the entangled floral organs. Nevertheless they show considerably greater independence than *Balsania diadema* and *B. Claviceps*, for directly after their appearance they no longer proceed to the formation of their perithecial heads, but rest for a period of several months. No longer does their tissue merge gradually with the stipe of the perithecial heads, but these soft plectenchymatic fertile parts are laid down under the rind of the sclerotia and become erumpent.

In the transition from *Balansia Claviceps* to *Claviceps balansioides*, the sclerotic plectenchyma fulfils special biological duties, especially of a



FIG. 162.—*Balansia Claviceps*. *A*. Habit. *Claviceps purpurea*. *B*. Sclerotia. *C*. Young sclerotium. *D*. Section of conidial layer. *E*. Germinating sclerotia. *F*. Perithecial head. *G*. Section of perithecial head. *H*. Section of perithecium. *J*. Ascus. *K*. Germinating ascospore. *L*. Conidial hypha from culture. (*A*, *B*, *E*, natural size; *J*, *K* × 350; *L* × 200, *after Tulasne, Brefeld and Lindau.*)

rest period of several months duration; but they are not independent in form, rather dependent to a high degree on the limits of their substrates.

This growing dependence of the sclerotia is shown in the Brazilian *Claviceps lutea* and *C. ranunculoides*. In *C. lutea* on *Paspalum* sp., the form of the sclerotia is still influenced by the substrate, but is much more independent than in *C. balansioides*, while in *C. ranunculoides* on *Setaria*, the sclerotia have become entirely independent of substrate and are able to form specific structures. In the young stage, their peripheral hyphae cut off orange-red conidia which disappear during the formation of the sclerotial rind.

The high point of this series is formed by *C. purpurea* and by *Ustilaginoidea*, differing chiefly in their imperfect forms. The Asiatic *Ustilaginoidea Oryzae* changes the ovaries of rice to pseudomorphs which cut off a large number of brown gemmae. These were earlier considered the smut spores of *Ustilago virens*. Although the perfect form of this species is unknown, the author believes that the resting over of the dry period by these gemmae suggests its relation to *Ustilaginoidea*, because in the South American species with the same gemmae, *U. Setariae* on *Panicum Crus-ardeae* (*Setaria Crus-ardeae*), true sclerotia are formed which, after a resting period, germinate with perithecial heads.

Claviceps purpurea, or ergot, is parasitic on various grasses, particularly rye. At flowering the ascospores infect the ovaries; which are permeated except at the tip by mycelium and transformed into dirty white, soft, furrowed pseudomorphs. On the surfaces of the furrows, the compact hyphal ends form a large number of small, unicellular hyaline conidia (Fig. 162, *D*) which, embedded in a sweet liquid, drop from the spikelet; they were described as the Imperfect *Sphacelia segetum*. Dissemination takes place by insects, occasionally also by rain and wind. They retain their ability to germinate and infect for more than one year (Stäger, 1912; Bonns, 1922). When this form of fructification has been exhausted, the body of tissue changes acropetally into a horny sclerotium which, because of a strong intercalary growth, projects out of the ear and is differentiated into a dark violet, rimose, pseudoparenchymatous rind and a prosenchymatous ground tissue. At its top, the hyphae of the *Sphacelia* stage grow luxuriantly; finally, they also dry and form a little cap at the tip of the sclerotia which contains the entangled and dried stamens and stigmas of the original flower (Fig. 162, *C*). When the life cycle of *Claviceps purpurea* was still unknown, this sclerotium was called *Sclerotium Clavus*. On drying, this becomes as hard as stone and forms the ergot or *secale cornutum* of the pharmacopoeia (Fig. 162, *B*). At maturity, the rye spikelets fall to the ground and winter over there in case they are not spread by man with the grain.

In the spring, with sufficient dampness, germination begins. Certain parts under the rind (in large kernels 20 to 30 of them) become rich in

protoplasm, divide much and grow to a column of tissue (Fig. 162, *E*) which ruptures the rind and develops the usual perithecial heads (Vincens, 1917; Killian, 1919). Sexual organs are formed in them in regular positions in the peripheral layer (Fig. 163) and are little differentiated from the surrounding vegetative tissues. Their first fundament consists of a multinucleate, elongate hypha, rich in protoplasm and arising from

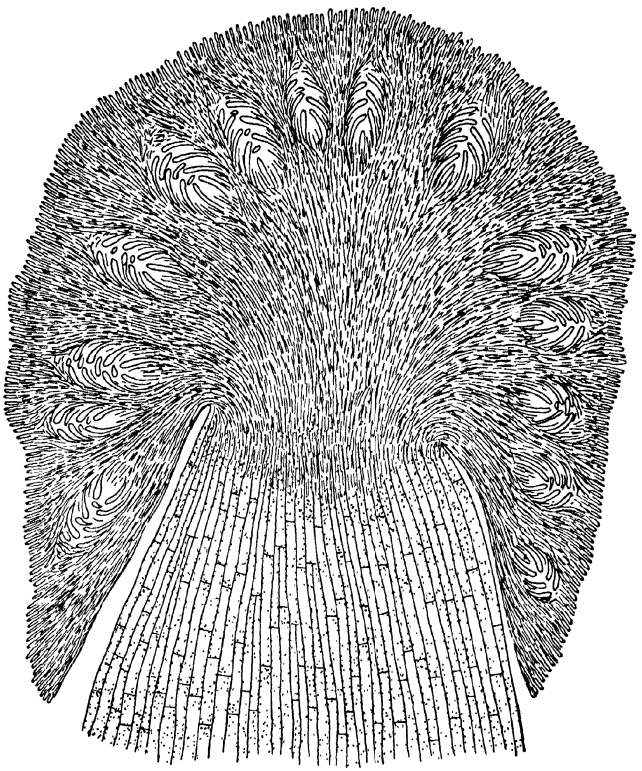


FIG. 163.—*Claviceps purpurea*. Diagrammatic section through a head showing primordia of perithecia. (*After Killian*, 1919.)

an empty vegetative cell (Fig. 164, 1). It is usually unbranched. The terminal cell swells, the nuclei divide and arrange themselves in pairs. They form two or three unicellular branches which bend toward each other and lie over one another (Fig. 164, 2). These branches take up the dicaryons, elongate considerably, and undergo repeated nuclear division; thereby the central branch, the future ascogonium, remains shorter and thicker; while the other branch (or both other branches), the future antheridium, is longer and more slender (Fig. 164, 3). The ascogonium

forms a small papilla on the side toward the antheridium (if there are two, toward the nearer) (Fig. 164, 4); the wall dissolves and the nuclei of the antheridium migrate into the ascogonium (Fig. 164, 5). The emptied antheridium collapses and disappears entirely.

On account of technical difficulties, the further development of the ascogonium is not yet cleared up. The numerous nuclei migrate from

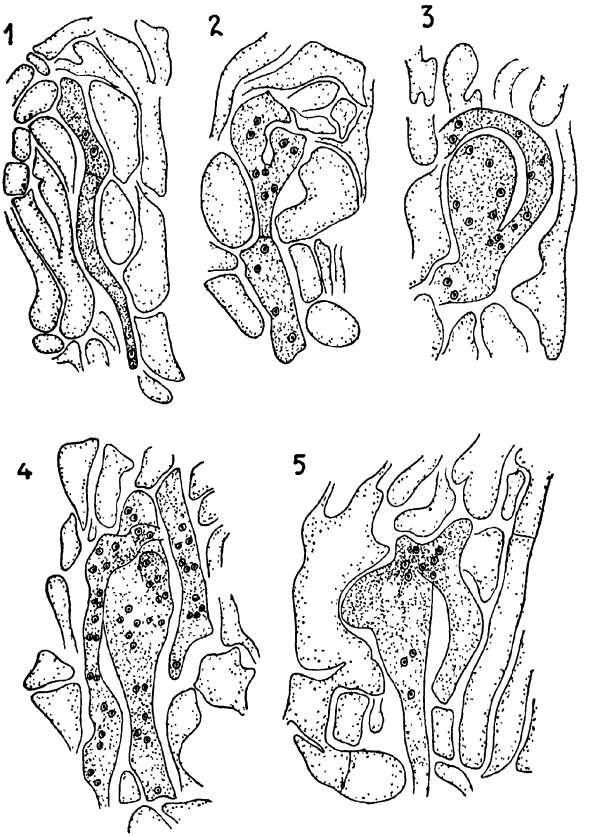


FIG. 164.—*Claviceps purpurea*. 1 to 3. Fundaments of sexual organs. 4. Ascogonium with copulation papilla. 5. Pasmogamy. (*After Killian*, 1919.)

the tip toward the base and the tip degenerates and disappears; of the ascogonium, there remains only a series of binucleate cells of unknown origin. These develop to ascogenous hyphae which form asci, according to the hook type. The ascospores again infect the ovaries of rye or other grasses in the range of hosts and mummify them.

The development of the sexual organs of *Claviceps purpurea* is reminiscent of *Monascus* in the Plectascales. As in the latter, a multinucleate

antheridium and ascogonium are formed on the same hypha; only in *Claviceps* there is no separation of a receptive organ, the trichogyne. The unusual degeneration of the tip of the ascogonium, however, may be connected with the fact that, like a trichogyne, it serves only for conception. In this case the trichogyne, although not morphologically present, might be functionally so. Furthermore, the development of the fertilized ascogonium of *Claviceps* is no longer independent, a fact which can only be more definitely formulated by subsequent investigations.

Our further knowledge of *Claviceps* is chiefly biological. In some of the biological strains peculiar changes of host occur because the main host is not in bloom when the sclerotia germinate (Stäger, 1905, *et seq.*). Thus the sclerotia on *Brachypodium silvaticum* normally germinate in the spring. At this time, the panicles of this grass are still deeply ensheathed so that infection is impossible. The fungus, however, can support itself by infecting the earlier-blooming *Milium effusum*, which grows with *B. silvaticum*, and produces the *Sphacelia* form on the

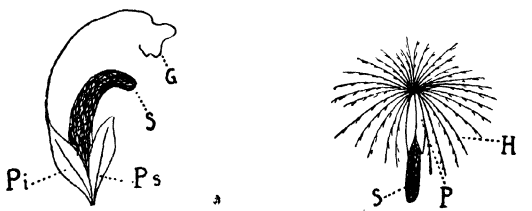


FIG. 165.—Method of dissemination of two kinds of ergot sclerotia. 1. Sclerotia between glumes of *Brachypodium sylvaticum*. 2. Sclerotia on *Calamagrostis epigeios*. *P*, palea; *Pi*, palea inferior; *Ps*, Palea superior; *G*, awn functioning as organ of attachment; *S*, sclerotia; *H*, Tuft of hairs. (*After Stäger*, 1922.)

former as an intermediate host, although the fungus rarely reaches the development of the normal sclerotia. Meanwhile *B. silvaticum* has bloomed, so that the fungus may complete its development there with the sclerotial formation. Thus both hosts are necessary. We will later meet relationships of this sort in *Sclerotinia* and in the Uredinales.

Interesting biological relationships have been found in connection with the dissemination of the sclerotia. While in the form *Claviceps purpurea* on rye, dissemination takes place mostly by man, *Claviceps* on other grasses often uses the dissemination mechanism of the host or, by its own adaptations, secures a passive motion in the surrounding medium. In the first case, in contrast to the ergot of rye, the sclerotia remain firmly attached between the glumes and then are spread by the host as if they were naturally developed ovaries. Thus, on *Brachypodium silvaticum* they utilize the awns for dissemination by animals (Fig. 165, 1); on *Calamagrostis epigeios* they utilize wind dispersal mechanisms of the host; in dry weather the umbellate crown of bristles at the base of the glume spreads, and with a breath of air the sclerotia are wafted away (Fig.

165, 2). In the second case, the sclerotia are indebted for their ability to spread to structural changes in their own tissue; thus in *C. Wilsoni* on *Glyceria fluitans* and in other aquatic and paludal forms (*e.g.*, on *Phrag-*

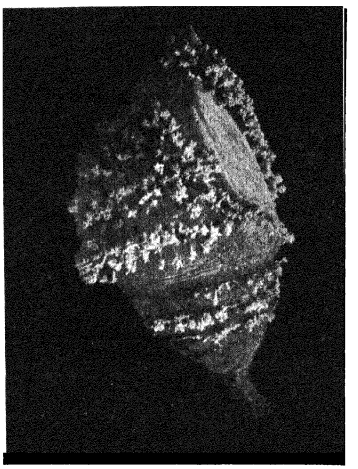


FIG. 166.—*Isaria* on *Morpho* pupa in Brazil. (Slightly enlarged; *after Möller*, 1901.)

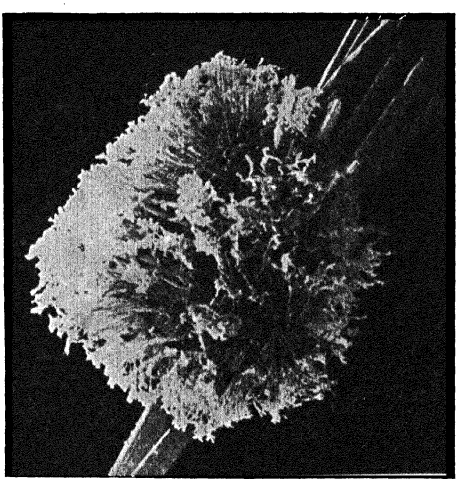


FIG. 167.—*Isaria* on pupa of hairy unknown species in Brazil. (Slightly enlarged; *after Möller*, 1901.)

mites communis and *Phalaris arundinacea*) the sclerotia, in contrast to those of the land plants, on account of enclosed air are able to float and are thus enabled to reach a suitable spot.

A representative of the third series of the Scolecosporeae is *Cordyceps*, which includes about 200 species and has fructifications of such a variation of structure that it is difficult to define them exactly. Most of them attack insects and only form perfect fructifications on substrates rich in proteins, as cadavers of insects or *Elaphomyces* fructifications. The biological relationships are not sufficiently clear; in any case they may be saprophytic; thus in Norway, the mycelium of *C. norvegica* on pine bombycid caterpillars is normally saprophytic in the forest floor and its parasitism is only facultative (Sopp, 1911).

Its imperfect forms belong to the *Verticillium–Penicillium* types and, as far as they appear on infected insects, are called *Muscardine*, which name is transferred to the disease itself. With sufficient nourishment, the conidiophores coalesce into graceful white or bright-colored coremia (Figs. 166, 167); they are classed in the Imperfect genus *Isaria*, *e.g.*, the coremia of *C. militaris* were called *I. farinosa*.

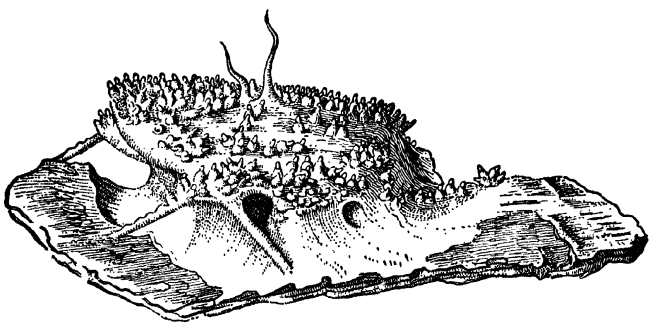


FIG. 168.—*Cordyceps rhynchoticola*. Habit, on dead leaf-louse. (× 3; *after Möller*, 1901.)

The perithecial stromata of the simpler forms, as in the Brazilian *C. rhynchoticola* found on dead leaf lice, are reminiscent of the higher species of the Amerosporae. *C. rhynchoticola* surrounds the cadavers with a loose hyphal felt, clings firmly to the substrate, and spreads out on it somewhat as in Fig. 168. The necks of the solitary, flask-shaped perithecia project over the stroma about 0.25 mm.

In the higher forms, as in all the Hypocreales, there occurs the differentiation of the stroma into fertile and sterile parts; the infected animal is penetrated in all directions by hyphae, mummified, and changed into a sclerotial structure from which later grow the perithecial stromata. In *C. norvegica*, they form a narrow clavate structure up to 20 cm. long on whose surface are imbedded the perithecia. It suggests *Clavaria pistillaris* of the Basidiomycetes. In the neighboring collective species, *C. militaris*, and in *C. ophioglossoides* on the fructifications of *Elaphomyces muricatus*, these clubs are again differentiated in a sterile base and fertile top (Fig. 169). In still others, especially in tropical

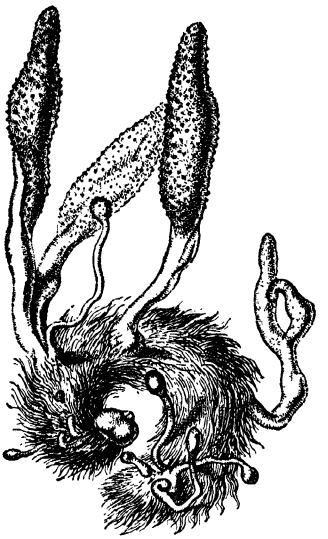


FIG. 169.—*Cordyceps militaris*. Habit, on dead caterpillar. (*After Tulasne.*)

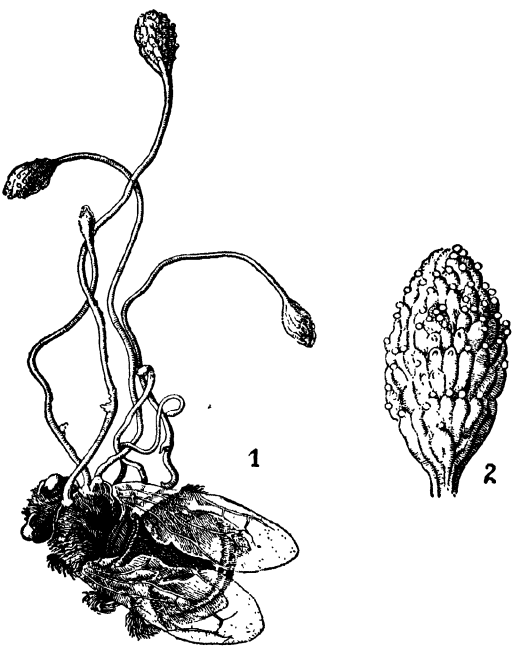


FIG. 170.—*Cordyceps thyrsoides*. 1. Habit, on dead fly in Brazil (× 2). 2. Perithe head (× 8). (*After Möller*, 1901.)

forms, these fertile parts have bizarre forms. Thus, in the Brazilian *C. thyrsoides*, the perithecia are obliquely imbedded in the rind so that the rind hugs each perithecium, thus forming cone-like structures in which the individual perithecia are like the cone scales (Fig. 170). In the Brazilian *C. Volkiana*, on lamellicorn larvae, there are formed from the bright yellow fructifications (in addition to the clavate perithecial heads) subulate or echinate processes on which the hyphae abstrict numerous hyaline conidia. This conidial formation gradually extends over the rest of the fructification, thus on *C. Volkiana* as on no other species of *Cordyceps*, the conidia and perithecia are formed on the same stroma.

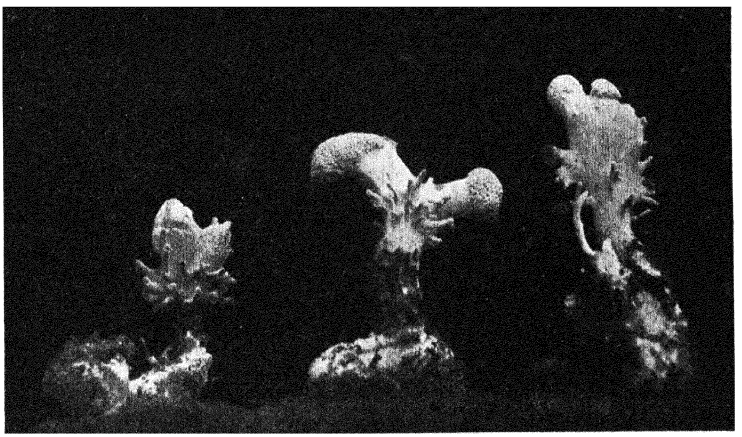


FIG. 171.—*Cordyceps Volkiana*. Habit, on lamellicorn beetle larvae. (About natural size; *after Möller*, 1901.)

With this peculiar form (Fig. 171), we conclude the third group of the Scolecosporeae and the Hypocreales. The phylogenetic significance of the Hypocreales lies in three different fields: imperfect forms, perfect forms and sexual organs.

The imperfect forms morphologically belong to the same types as the Plectascales; they unite into fructifications to a higher degree, however, and undergo a many-sided development which in the parasitic species ends in stromatic forms (*Tuberculariа* and *Sphacelia* types), in coremia (*Sphaerostilbe* group) and in pycnia (*Polystigma* and some species of *Nectria*), and in the saprophytic forms leads to structures (*e.g.*, in the *Isaria* group) which are equal in beauty to the perfect forms.

Also the perithecia show the same sort of structure as in the Plectascales and Perisporiales; they unite, however, in a higher degree to stromatic complexes and as such undergo special development to new aggregate fructifications, which gradually differentiate into fertile and

sterile parts. In the saprophytic group, the high point is reached by *Ascopolyporus* and its relatives which are equivalent to the higher Polyporales; in the parasitic species, the high point is reached by the *Claviceps* group which, through an extensive biological differentiation of its sterile (*i.e.*, the parts forming imperfect forms) and of its fertile parts, attains to types which are unique among fungi. In many lower forms, as *Nectria* and *Corallomyces*, the conidia and perithecia arise successively on the same stromata while in the higher forms the conidial and perithecial stromata are developed separately (*e.g.*, *Isaria–Cordyceps* group) and in part also differ biologically (*Sphacelia–Claviceps*).

As all these fructifications of the perfect stage are to a certain degree compound fructifications, it is not surprising that the original solitary perithecia which have secondarily collected to an aggregate fructification (stroma) gradually merge their individuality in this stroma. While they originally were formed with a well-developed wall on or in the stromata, in the immersed forms this wall is no longer a protection and gradually degenerates, and the perithecia are no longer differentiated from the ground tissue but as schizogenous cavities in the periphery of the stromata.

The sexual organs of the Hypocreales are connected to those of the Plectascales and Perisporiales. In the former, the antheridium, which is still present in some of the lower forms and possibly still functional, is rapidly lost and the ascogonium develops alone. Caryogamy is not entirely suppressed, but, instead of cross fertilization, for the first time in the fungi under discussion, parthenogamy occurs between two cells of the ascogonium. Thus begins a series of deuterogamous forms which will occupy us until we finish the fungi.

CHAPTER XVII

SPHAERIALES

The Sphaeriales when first described as an order were regarded as a series parallel to the Hypocreales from which they differ in their dark-colored, leathery, hard or carbonaceous perithecia, always independent within the stroma. Recent investigations have shown that this conception suits only a portion of the order, while another portion differs entirely in the direction of development; thus the Sphaeriales belong to the few orders of fungi whose existence is no longer justified.

The first type in the Sphaeriales, which corresponds to the dark-colored, hard Hypocreales, is designated as the *Diaporthe* type (Höhnel, 1917). In addition to lacking paraphyses, it is characterized by asci which stand at unequal heights and hence entirely fill the cavities of the perithecium. At maturity, their bases swell and then are held together only by a gel which is easily soluble in water; hence they generally separate in preparations and float away in the mounting fluid.

Another group, differing phylogenetically, has a core of the *Pseudosphaeria* type, *i.e.*, of paraphysoids in the lower forms, and of true paraphyses in the higher forms. Still other groups, as the Coryneliaceae and certain Diatrypaceae (Coronophoreae), belong to other phylogenetic groups which are still vaguely defined.

Because of this obscurity the systematic classification of the Sphaeriales, as created by Winter (1887), Jaczewski (1894) and Lindau (1897), and on which the following discussion is based, must be treated in artificial units, which have greatly facilitated the arrangement of an enormous amount of material, but which, because they separate phylogenetically related forms, make difficult the recognition of relationships. As a basis of this artificial systematic classification, purely empiric characters are used, as the structure and occurrence of the fructifications of the perfect forms, the perithecia. Their phylogeny, their internal structure and imperfect forms, however, have so far been much neglected. Hence, in only the rarest cases is it possible to recognize phylogenetic relationships between the different families.

Sordariaceae.—This family includes genera with flask-shaped perithecia with thin walls, rarely horny, without stromata (Fig. 82). The members are chiefly coprophilous or otherwise saprophytic.

As far as their development is known, it agrees with the simple Hypocreales and Plectascales. Thus in *Chaetomium globosum* (*C. Kunzeanum*)

and some relatives (like *Aspergillus herbariorum*) a helical ascogonium is formed, from whose stipe springs an antheridium which climbs along the helix. At times the antheridium may also be lacking (Oltmanns, 1887). In some species of *Sordaria* (as in *Penicillium crustaceum*) antheridium and ascogonium coil helically (Nichols, 1896). In some other forms as *Chaetomium spirale, C. globosum* (*C. Kunzeanum var. chlorinum*) (Vallory, 1911), *Sordaria fimicola* (*Fimetaria fimicola*), *S. merdaria* (*F. merdaria*) and *Podospora hirsuta* (*Pleurage hirsuta*), as in *Aspergillus flavus* and *A. fumigatus*, only an ascogonium is formed which develops in an unknown manner to ascogenous hyphae (Dangeard, 1907). Only for *Sordaria macrospora* (*Pleurage macrospora*), *Sporormia intermedia* (Dangeard,

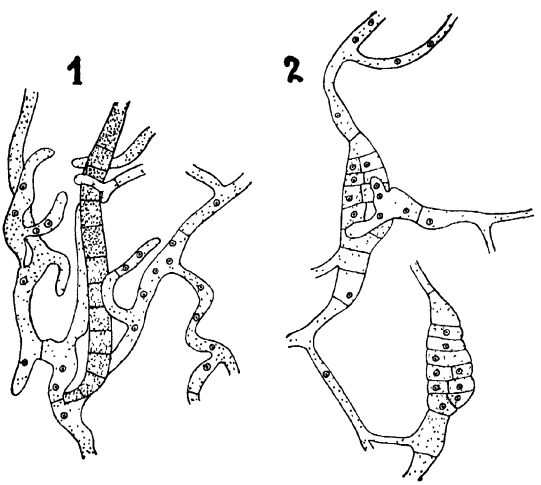


FIG. 172.—*Sordaria macrospora*. 1. Elongate ascogonium with sheath hyphae. *Sporormia intermedia*. 2. Young perithecial fundaments, the upper showing an antheridium. (*After Dangeard*, 1907.)

1907) and *S. leporina* (Delitsch, 1926) has a new, peculiar relationship been determined. In the former the ascogonium is not coiled but vertical (Fig. 172, 1) and divided into several short multinucleate cells. In the latter a typical ascogonium is no longer formed. A hyphal cell becomes barrel shaped (Fig. 172, 2) and is septate in three dimensions to a small node. At times before it is septate, a hyphal branch approaches it and anastomoses with it, but details of the process, as those of *Sordaria macrospora*, are unknown.

According to the structure of the mature fructifications, the Sordariaceae may be divided into two tribes, the Chaetomieae and Sordarieae; in the former the perithecia are generally covered with a thick felt of spiral or forked hairs, which the latter lack; these differences, however, are quantitative.

There are three genera in the Chaetomieae, *Chaetomidium*, *Ascotricha* and *Chaetomium;* the first is distinguished by the lack of an ostiole and thus shows its relationship to the saprophytic Perisporiaceae; the second by a neck with ostiole crowned by a tuft of hairs; the last includes those with ostiole without tuft of hairs and neck (Bainier, 1909; Chivers, 1915). They occur chiefly on dung and decaying plants. Their imperfect forms are very manifold; thus in *Chaetomium Boulangeri* are formed *Graphium* coremia with a dark brown to black stipe up to 20 μ thick which

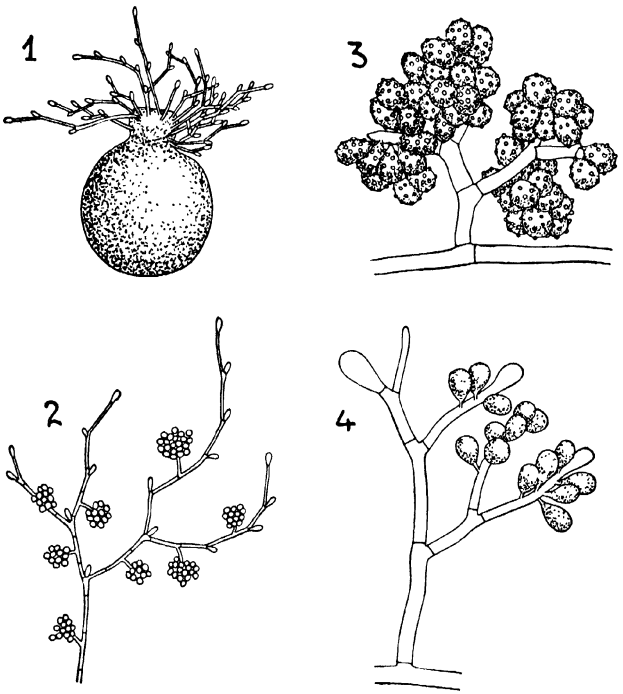


FIG. 173.—*Ascotricha chartarum*. 1. Perithecium with setae about the ostiole. 2. Conidiophore of *Dicyma* form. 3. Branch of conidiophore. 4. Conidiophore of *Sporotrichum* form. (1 × 105; 2 × 60; 3, 4 × 980; *after Boulanger*, 1897.)

disappears above in a broom-like, lighter-colored and finally hyaline fertile part (Lindfors, 1920). In *Ascotricha chartarum* (*C. Zopfii*) on the rind of *Piscidia erythrina* (Boulanger, 1897), two imperfect forms have been discovered, one a *Sporotrichum* type with smooth, hyaline conidia (Fig. 173, 4) and a *Dicyma* type with echinulate, ovoid, thick-walled, dark brown gemmae (Fig. 173, 3). These, on dark-colored, sympodially branched conidiophores (Fig. 173, 2), appear deceptively like the sterile bristles on the neck of the perithecium. In other Chaetomieae, other conidial forms have been noted (thus *Verticillium*, etc.).

While the Chaetomieae in *Chaetomidium* probably show the root of the family, the Sordarieae (Griffiths, 1901; Griffiths and Seaver, 1910) in *Sporormiella* and in some species of *Sordaria* (subgenus *Hypocopra*) in which the perithecia (as in the higher *Melanospora* species of the Hypocreales) are embedded in the stromata and extend in the direction of the stromatic Pyrenomycetes. The Sordarieae also are richer in

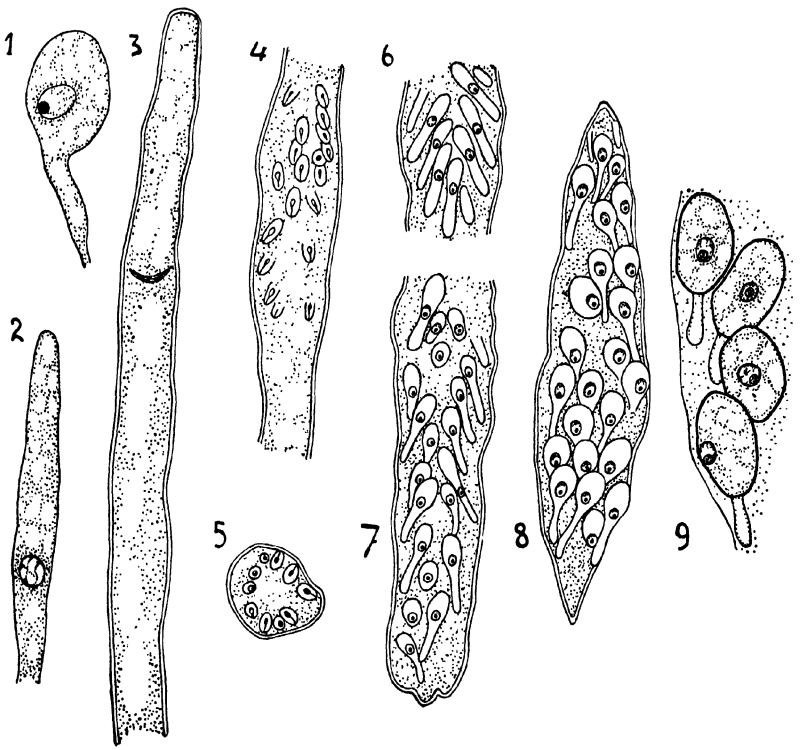


FIG. 174.—*Philocopra coerulcotecta*. Development of ascospores. 1. Young ascus with primary nucleus. 2. Elongated ascus. 3. First division of primary nucleus. 4. Ascus with young spores. 5. Section of young ascus. 6. Swelling of upper end of ascospores. 7, 8. Older stage. 9. Mature ascospores with stipe cell. (1, 4 to 7, 9 × 800; 2, 3, 8 × 920; *after Jolivette-Sax*, 1918.)

forms than the Chaetomieae and thus show more peculiar relationships, especially in the structure of their ascospores. In *Sordaria* (*Fimetaria*) and in *Podospora*, *Philocopra* (*Pleurage*) the ascospores are usually unicellular, in the former provided with a hyaline gelatinous sheath, in the latter with two or more gelatinous appendages. In many species they subsequently undergo a further development; in *Philocopra caeruleotecta*, there are first laid down 128 thin-walled spherical ascospores which elongate (Fig. 174, 1 to 6). The nucleus of each migrates to the upper end which

swells clavately, thickens, browns its wall and is abjointed from the enucleate hyaline lower part (Fig. 174, 7 to 9) (Jolivette-Sax, 1918). In *Philocopra zygospora*, they elongate to many times their original length and undergo several nuclear divisions, whereby in time they generally lay down several septa (Lewis, 1911). The two end cells (always uninucleate) swell strongly, thicken their wall, form echinulate appendages and develop to true spores (Fig. 175, 5), while the intermediate part gradually dissolves. Functionally, 16 ascospores are formed, morphologically, only 8.

It is possible that these two types were originally from scolecosporous ancestry and that we have in them a special differentiation of

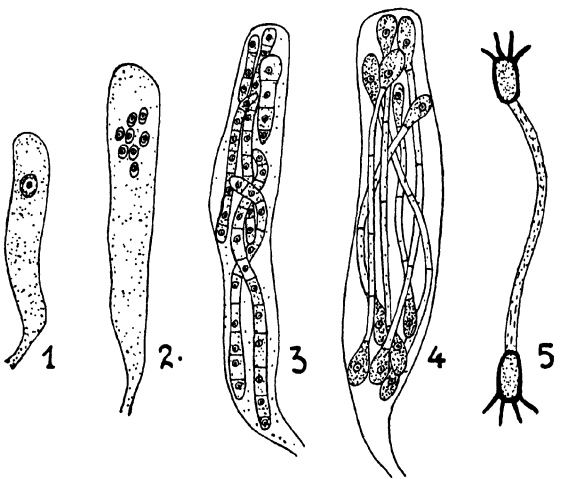


FIG. 175.—*Philocopra zygospora*. Development of ascospores. 1. Young ascus with diploid nucleus. 2. Ascus with eight young ascospores. 3. The ascospores have developed to septate filaments. 4. Showing the swelling ends of the ascospores. 5. Mature, three-celled ascospore. (× 590; *after Lewis*, 1911.)

Epichloe-like, septate spore chains. Unfortunately, too few representatives of this type have been investigated cytologically; a beginning or end member of this developmental series is possibly *Podospora anserina* whose ascospores are said to be always binucleate (Wolf, 1912). In other genera, the ascospores remain multicellular, as bicellular in *Delitschia*, quadri-multicellular in *Sporormia*. Imperfect forms are rarer in the Sordarieae. In cultures *Podospora Brassicae*, on short branches, cuts off hyaline conidia which unite into large heads; *Sporormia megalospora* forms pycnia with bacilliform, hyaline conidia (Brefeld, 1891).

While in the Sordariaceae, the perithecia are generally fleshy to membranous and hence appear like the simpler Hypocreales, as species of *Melanospora*, in the following families they are formed as in true

Sphaeriales, *i.e.*, they are leathery, woody or carbonaceous and generally fragile. Next will be discussed a group of families in which the perithecia are formed on the surface of either the substrate or the stroma. Of the group on the surface of either the substrate, are the Sphaeriaceae and Ceratostomataceae; in the former the perithecial opening is generally short, papilliform, in the latter it is long necked or even drawn out like a hair.

Sphaeriaceae.—This family is divided into two tribes, the Trichosphaerieae (perithecia covered with hair on the whole surface or at least at the base) and the Melanommeae (perithecia smooth). There are more than one thousand species, generally saprophytic on wood, bark, tree trunks, etc., more rarely parasitic. They cover large stretches of the substrate with a turf, causing it to appear as if gunpowder were scattered over it. The only genus of economic significance is *Rosellinia*, whose hairy (as in the Trichosphaerieae) or naked (as in the Melanommeae) fructifications occur both singly and gregariously, and are also gregariously immersed in a loose hyphal felt; in the saprophytic forms they often seem like those of the Sordariaceae. *Rosellinia necatrix* is a very dangerous parasite on roots of the vine and pleached trees. As those of many other subterranean fungi, its rhizomorphs—white in the vegetative stage or brown in age—penetrate the interior of the root, kill it and live on it saprophytically (*Dematophora* form). In this condition, on black sclerotial hyphal knots they form their brown conidiophores which cut off hyaline conidia on their ultimate branches. In the course of the year, they form the perithecia on the rotting roots (Prillieux, 1904). These are hard and carbonaceous; at maturity the paraphyses and the ascus wall gelify, the perithecial papilla is thrown off like a stopper by the tearing of a dehiscence zone and the brownish black ascospores exude in a drop of slime. *R. quercina* is known as a root disease of oaks; another species, as the gray root fungus of the Javan cinchona plantations; the former forms massive black sclerotia, the latter chiefly *Graphium* coremia.

Ceratostomataceae.—This family is best known as a saprophyte on the woody parts of plants, economically important as the cause of sap stains, bluish discolorations of lumber which do not greatly alter the strength of the timber. Two common species, *Ceratostomella pilifera* and *C. echinella*, have the form genus *Graphium* as an imperfect stage. *C. fimbriata*, the cause of black rot of the sweet potato, has an imperfect stage formerly known as *Sphaeronema fimbriatum*. There seems a slight suggestion of heterothallism since antheridia and ascogonia arise from separate hyphal strands. The antheridium coils about the ascogonium, which is differentiated in a basal cell, ascogonium and trichogyne, the latter continuous with the ascogonium. The trichogyne may fuse at any point it comes in contact with the antheridium, the single male nucleus migrates into the ascogonium and fuses with the female

nucleus. After a considerable resting period the fusion nucleus divides to form eight nuclei; the nuclei pair and migrate into the developing ascogenous hyphae.

During the resting stage of the fertilized ascogonium large thin-walled cells arise from the basal cell of the archicarp and partially fill the developing perithecium which is formed from hyphal branches of the ascogonial branch. The ascogenous hyphae branch throughout the perithecial cavity between the thin-walled sterile cells and fuse with them or, if sterile cells are not well developed, with the inner cells of the perithecial wall, reminding one of the fusions with auxiliary cells by the oöblastema filaments in the Florideae. The connections with the original ascogonium disappear, so that by the time the perithecia are matured, the ascogenous cells appear to be arising from the perithecial walls. The asci are first developed basipetally from the top of the perithecium simultaneously with the beak. No hook formation occurs, the asci being terminal on short branches. The young ascus is binucleate, then the nuclei fuse to a fusion nucleus about half the size of the fusion nucleus of the ascogonium. This nucleus divides into eight nuclei which form ascospores about themselves in the usual manner. While the ascospores are still immature the asci disappear leaving the eight more or less associated spores to continue their development in the perithecium (Elliott, 1925).

In *Ceratostoma brevirostre*, the unicellular ascogonium is coiled and lacks a distinct trichogyne. It becomes septate and develops ascogenous hyphae (Nichols, 1896).

In the first group, with perithecia on the upper surface of the substrate, certain genera, especially the Trichosphaericae of the Sphaeriaceae, show a tendency to unite their perithecia on stromata. These forms lead to the second group which normally forms its perithecia on stromata, the Cucurbitariaceae and Coryneliaceae. This coincidence is only external, however. One cannot argue that these stromatic forms (as the stromatic Nectriaceae) have arisen as composites by the crowding of solitary perithecia with a subiculum, but must assume that they belong to essentially different groups, the former to the Dothioraceae–Pseudosphaeriaceae line, the latter to the Perisporiales lines; both families have attained the height of their development in the tropics and hence are poorly known.

Cucurbitariaceae.—The perithecial stromata of this family vary from a thin subiculum to a thick, pulvinate stroma upon which the perithecia are borne. The bases of the perithecia are often partially immersed in the stroma, which is erumpent from the bark. Some species of *Cucurbitaria* are wound parasites of roots and branches, as *C. Laburni* on *Laburnum* and *C. Berberidis* on barberry (Welch, 1926). In the chiefly tropical *Nitschkia* (Fitzpatrick, 1923), the perithecia collapse at maturity and, seen with a hand lens, seem like the mature fertile branches of *Myrian-*

gium (Fig. 137, *B*). Some of them, as *N. cupularis* on the dead branches of frondose species, generally do not have true stromata, but only a subiculum.

Coryneliaceae.—The perithecial turf (Fitzpatrick, 1920) is chiefly hypodermal and erumpent. In the simplest genera, as *Caliciopsis*, the perithecia seem like those of the other Sphaeriales, and rest upon stipitate outgrowths of the stroma; some species of *Caliciopsis* are saprophytic on the dead bark of frondose trees, others are parasitic on conifers where they form pycnia and perithecia successively in the same stroma. In *Psorica*, on ferns, the perithecia are still stipitate, but become allantoid. In *Corynelia* and *Tripospora*, chiefly on *Podocarpus* leaves, the perithecia are sessile, flask shaped, allantoid, elongated to several times their original length. All these genera have no true ostiole, but tear open at the tip in a predetermined manner. In the lower forms, the hyphal elements easily pull apart, leaving a ciliate opening. In the higher forms, deep dehiscence lines are already formed so that a perithecium opens by a sharply defined slit; in one species only one slit is formed, in others often several radial slits, so that three or more lobes result. Often the slit is so large that the whole interior of the perithecium is laid open. In some species of *Corynelia*, the lobes are thrown back like discs so that there arises on the top of the allantoid perithecium a flat plate-like bowl.

Through this lack of a true ostiole and presence of a highly specialized manner of opening, the Coryneliaceae are entirely out of the general scheme of the Sphaeriales; until one knows more of their phylogeny, however, it is impossible to associate them elsewhere.

While these four first families are distinguished by perithecia superficial on substrate or stroma, the following families are characterized by perithecia which are either partially (at the base) or wholly imbedded in the substrate or stroma.

Of the half-embedded forms, two families may be mentioned, the Amphisphaeriaceae (with round ostioles) and the Lophiostomataceae (with laterally compressed ostioles); the former are of interest by their transition from asterinoid habit to epiphytism; the latter, as the connecting link to the Hysteriales. As the Lophiostomataceae are only imperfectly known we will limit ourselves to the Amphisphaeriaceae.

Amphisphaeriaceae.—These have, as in the *Thielavia* group of the Aspergillaceae, the *Meliola–Parodiopsis* group of the Perisporiaceae and the endophytic-ectoparasitic series of the Erysiphaceae, passed over to ectoparasitism in damp, warm climates and finally to pure epiphytism. Hence they have attained to the formation of characteristic vegetative forms which, on account of their special habit, bear the name of sooty moulds. They are especially closely connected in habit and morphology to the Perisporiaceae and generally are grouped with the latter; but it seems to me (although some of its representatives have no ostiole) that they are

better placed with the Sphaeriales as by Arnaud (1910, *et seq.*). As they are extremely pleomorphic and often several genera appear adjacent or intermingled on the same substrate, only extensive cultural investigations can make clear their forms.

Pleosphaeria Citri (*Limacinia Citri*) in the Mediterranean region is an epiphytic, sooty mould on the leaves and twigs of *Citrus*, *Nerium*, *Laurus*, etc., and especially luxuriant on the honey dew of leaf lice. The mycelium is comparatively light colored, developing, according to growth conditions, to a thin subiculum on which rest the pycnia and perithecia, or to a luxuriant but loose subiculum in which are embedded the organs of fructification. Both the pycnidia and perithecia are surrounded by erect setae. A view of the structure of the perithecium is shown in Fig.

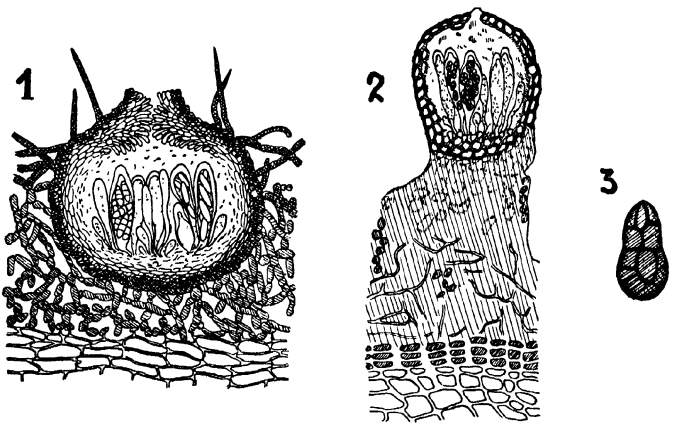


FIG. 176.—*Limacinia spongiosa*. 1. Section of perithecium and subiculum (× 200). *Teichospora meridionalis*. 2. Perithecium with disintegrating subiculum (× 200). 3. Ascospore (× 670). (*After Arnaud*, 1911.)

176, 1, which gives a longitudinal section of a species closely allied to *Pleosphaeria Citri*, the also epiphytic *Limacinia spongiosa;* it is to be observed that the perithecia are still normally embedded in the flat subiculum.

In other genera there appears a peculiar tendency, as in many Myriangiales, to raise the perithecia on plectenchymatic protrusions above the stroma, which thus is differentiated into sterile basal and fertile columnar parts. A schematic cross section through a similar transitional form, *Teichospora* (*Capnodium*) *meridionalis*, also on *Nerium* and *Citrus*, is shown in Fig. 176, 2. Under suitable growth conditions, its subicular hyphae swell and in damp air become slimy, adhere in a slimy stroma which occasionally exhibits very bizarre forms.

We may consider as an end form of this developmental series *Teichospora* (*Capnodium, Apiosporium,* and *Fumago*) *salicina,* a black

mould on the leaves of willow, poplar, rose, greenhouse plants, etc. All possible imperfect forms have been ascribed without their appropriateness

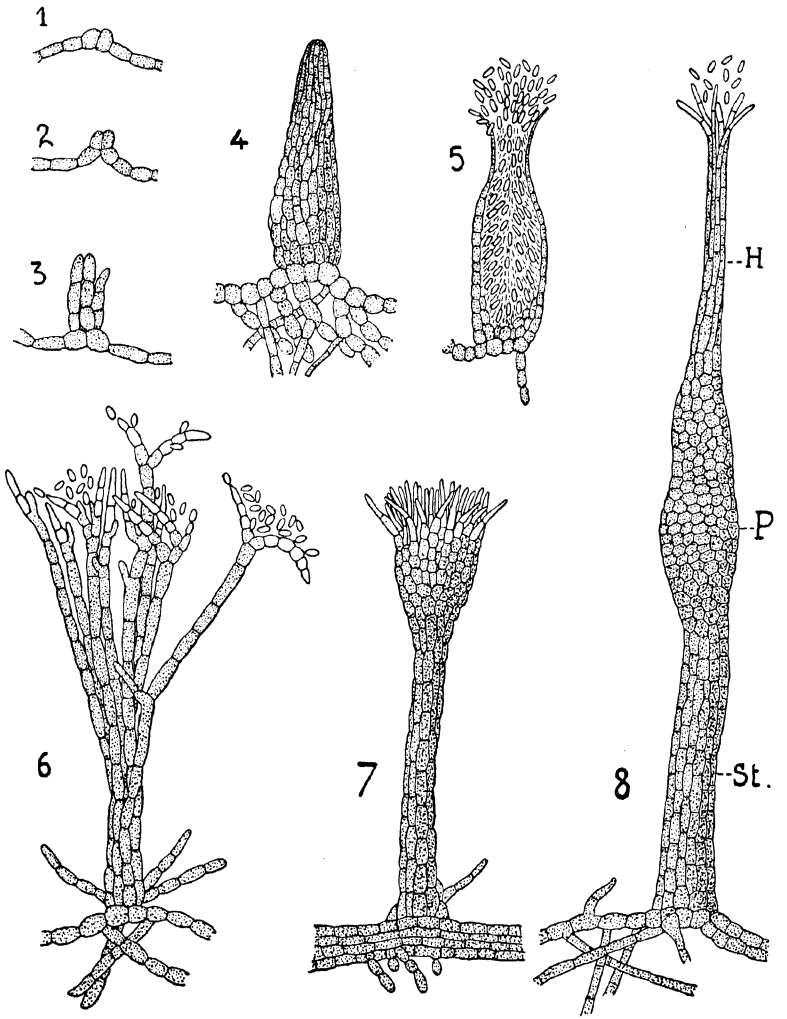


FIG. 177.—*Teichospora salicina*. 1 to 4. Fundaments of a pycnium. 5. Section of sessile pycnium. 6. Tuft of conidiophores. 7. Coremium closing up to form a stipitate pycnium. 8. Stipitate pycnium, St, Stalk; P, pycnium; H, neck. (× 360; *after Zopf*, 1878.)

being culturally determined. Their mycelium develops by sprouting in sugar solutions, as on honey dew in nature, occasionally forming clumps of dark brown resting cells, **coniothecia**. Except for this gemma-like

imperfect form, there occur erect, single, generally branched conidiophores which cut off ovoid conidia at their ends (Fig. 177, 6). They may come together into columnar coremia, whereby they are oriented with bilateral symmetry and abjoint conidia only on the inner side (Fig. 177, 7). With sufficient nourishment, these coremia differentiate to pycnia in which the formation from individual hyphae is still more marked (Fig. 177, 8) and hence have been called hyphal pycnia; besides the tissue, pycnia are formed (Fig. 177, 1 to 5) with true paraplectenchymatic walls (Zopf, 1878). The perithecia, like the stipitate pycnia (Fig. 177, 8), arise on a black, occasionally branched columnar foot, and show a structure similar to that given in Fig. 176, 1 and 2 for *Limacinia spongiosa* and *Teichospora meridionalis*.

In spite of their frequency, all these epiphytic Amphisphaeriaceae are known neither culturally nor phylogenetically. It is only certain that in a species of *Teichospora* and one of *Teichosporella*, and in *Pleosphaeria Citri*, the perithecia arise, as in *Sporormia intermedia*, by the division of a single hypha in three planes (Nichols, 1896; Arnaud, 1910).

The completely submersed Sphaeriales include most of the group and occur in thousands of tiny, generally very monotonous species on leaves, roots, etc. There are two families without stromata, the Mycosphaerellaceae (with asci not thickened at the tip) and the Gnomoniaceae (with asci thickened at the tip and opening by a pore).

Mycosphaerellaceae.—Among this family are also reckoned the earlier "Pleosporaceae" except those belonging to the Pseudosphaeriaceae, as *Pleospora* itself; this union of the Pleosporaceae and Mycosphaerellaceae seems justified since the presence or absence of paraphyses is hardly sufficient to separate families.

This family has a special significance in its relationship to the Myriangiales; thus they have (in the old concept including the Pleosporaceae) supplied the main group of the Pseudosphaeriaceae; similarly *Didymella* and *Leptosphaeria*, which were discussed at the close of the Myriangiales, earlier belonged to the Mycosphaerellaceae. The continuity of the Pseudosphaeriaceae and Mycosphaerellaceae is secured through *Mycosphaerella* of the Mycosphaerellaceae which, through various transitional forms, are continuous with *Leptosphaeria* and *Didymella;* thus in some species of *Mycosphaerella* we find a scant, hyaline, insignificant perithecial stroma, while other species possess true perithecia of the Sphaeriales.

Mycosphaerella, with over 1,000 species parasitic on all sorts of plant substrates, generally forms its fructifications after wintering over under the epidermis of dead and rotting tissue. According to the type of its imperfect forms, it may be divided into several sections: *Septorisphaerella* with *Septoria*, or *Phleospora* as imperfect forms, *Ramularisphaerella* with *Ramularia* conidia and *Cercosphaerella* with *Cercospora* (Klebahn, 1918).

To *Septorisphaerella* belong *Mycosphaerella Hippocastani* (*Carlia Hippocastani*), a leaf spot of *Aesculus Hippocastanum*, and *M. sentina*, a leaf spot of pear. As imperfect forms besides pycnia with multicellular conidia (*Septoria aesculicola*), Klebahn (1918) found in culture free falcate conidia similar to *Septoria* conidia which are cut off laterally on hyphae and also pycnia with very small bacilliform microconidia.

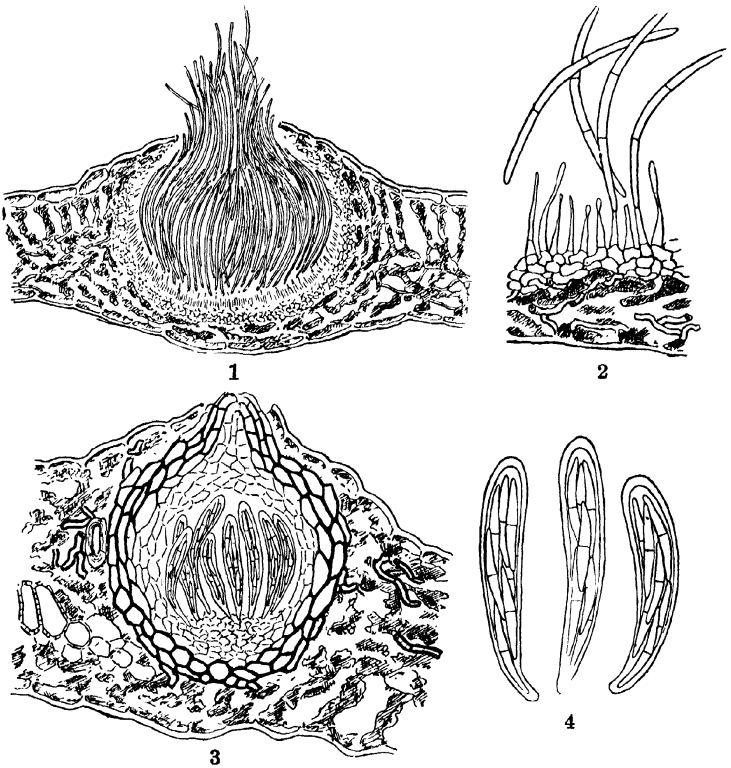


FIG. 178.—*Mycosphaerella sentina*. 1. Pycnial stage. *Septoria pyricola*. 2. Part of perithecial wall. 3. Perithecium. 4. Asci with ascospores. (1 × 236; 2, 4 × 550; 3 × 460; *after Klebahn*, 1908.)

Septoria pyricola is the only imperfect form of *M. sentina* (Fig. 178, 1) (Klebahn, 1908; Laibach, 1920).

Of the section *Ramularisphaerella*, *M. Fragariae*, *M. punctiformis* and *M. Hieracii* are worthy of note. *M. Fragariae*, a leaf spot of strawberries, has *Ramularia Tulasnei* (Schellenberg, 1917). *M. punctiformis*, a leaf spot of *Tilia*, forms free conidiophores with catenulate conidia, pycnia and perithecia. *M. Hieracii* winters over on *Hieracium*, like *M. Fragariae*, with small black sclerotia which grow into the rind of the stem

and germinate in spring, producing conidia of *Ramularia Hieracii* (Klebahn, 1918).

Of *Cercosphaerella, M. millegrana* on leaves of *Tilia cordata*, forms conidia of *Cercospora microsora* and, further, the imperfect form of *M. cerasella*, a leaf spot of cherry, is *Cercospora cerasella* (Aderhold, 1900).

As has been indicated, the extent of the imperfect forms of *Mycosphaerella* is by no means exhausted in the three sections above; *e.g.*, of the forms important in phytopathology, *M. pinodes*, causing a spot of pods of beans and peas, has *Ascochyta Pisi* (Vaughan, 1916) and *M.*

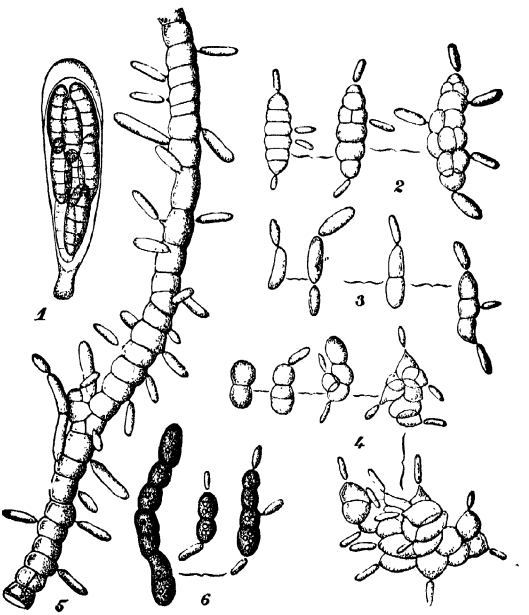


FIG. 179.—*Sphaerulina intermixta*. Its growth forms known as *Dematium pullulans*. 1. Ascus with mature spores. 2. Ascospores developing sprout mycelium in nutritive solution. 3. Sprout cells. 4. Sprout cells developing in groups. 5. Hypha forming sprout cells. 6. Sprout cells changing to chains of gemmae. (× 350; *after Brefeld.*)

tabifica causing dry heart rot and leaf spot of beets and sugar beets, has *Phoma Betae*, on the roots, and *Phyllosticta tabifica* in the leaves as its imperfect forms.

In the remaining purely "sphaerial" Mycosphaerellaceae, only four pathogenic genera are discussed: *Venturia* (ascospores, as in *Mycosphaerella*, divided into two equal cells, perithecial hairy, paraphyses present), *Guignardia* (ascospores divided into two unequal cells), *Dilophia* and *Sphaerulina* (ascospores multicellular). *Venturia inaequalis* causes apple scab; its imperfect form is *Fusicladium dendriticum*. *Guignardia Bidwellii* causes black rot of grapes; it forms micro- and macroconidia in

separate pycnidia like *M. Hippocastani*, and *Guignardia Aesculi* (Stewart, 1916), which in the United States causes leaf blotch of horse chestnut as *M. Hippocastani* in Europe. *Dilophia graminis* is regarded as the perfect form of *Dilophospora graminis* which causes the *Dilophospora* disease of wheat. *Sphaerulina intermixta* is saprophytic on dry branches on roses and blackberries and *S. Trifolii*, the *Sphaerulina* leaf spot of clover. In *S. intermixta*, Brefeld (1891) reports that the hyaline ascospores may develop, immediately after ejaculation, to a sprout mycelium (Fig. 179, 2) which under certain conditions swells into an amorphous cell clump (Fig. 179, 4). The same sprout cells may also be cut off by the hyphae. After exhaustion of the nutrient solution, the sprout cells change into bi- or multicellular gemmae which, under certain conditions, develop to long, brown chains at times intertwined to papery membranes (Fig. 179, 6). Their ability to germinate is not injured by drying and is retained more than 1½ years. Under normal conditions, they germinate to a hyaline sprout mycelium or with germ tubes. This type of germination has not been reported elsewhere in the group and probably was based on impure cultures.

Cytologically, in contrast to the previous families, there is a large amount of investigation in the Mycosphaerellaceae. Higgins (1914, 1920) investigated *M.* (*Septorisphaerella*) *nigerristigma*, on leaves of *Prunus pennsylvanica* and *M.* (*Ramularisphaerella*) *Bolleana* on leaves of *Ficus carica*, and found in them, as in *Polystigma*, a helical ascogonium with a functionless trichogyne. Killian and Likhité (1923) and Likhité (1926) in a species on *Salix caprea* (judging from the figures, probably *Mycosphaerella* with the imperfect form described as *Hendersonia foliorum*) have observed that the helical ascogonium, as in *Polystigma*, is divided into a sterile basal and a fertile apical, multinucleate portion. Degeneration of sterile and fertile portions proceeds until only one or two cells remain, from which ascogenous hyphae develop in the usual manner.

Finally Killian (1917) has reported still functional antheridia in *Venturia inaequalis*. As this species has been investigated more fully, its life cycle is given in detail. Its mycelium lives between epidermis and cuticle in the leaves of the apple. The formation of brown conidiophores (*Fusicladium dendriticum*) ruptures the cuticle and finally peels it off. Thereby the transpiration of the cells beneath increases, and they dry out. The fungus begins to grow during the summer, and forms a small, brown, round, woolly covering with characteristic dendritic indentations. In the fall the mycelium in the older middle part of the cover begins to die off. In this spot the injured leaf surface is discolored and gray. The leaves are scurfy, yellow and fall off early in October before the healthy ones.

In the peripheral parts, the ageing hyphae remain alive and grow to a plectenchymatic tissue. In November, when the leaf is entirely dead and

the inner tissue is considerably altered and crumbled, the peripheral hyphae awake to new life and penetrate the crumbling interior of the leaf. Earlier, when the leaf was alive, they could only penetrate between epidermis and cuticle but they now penetrate the dead tissue in all directions.

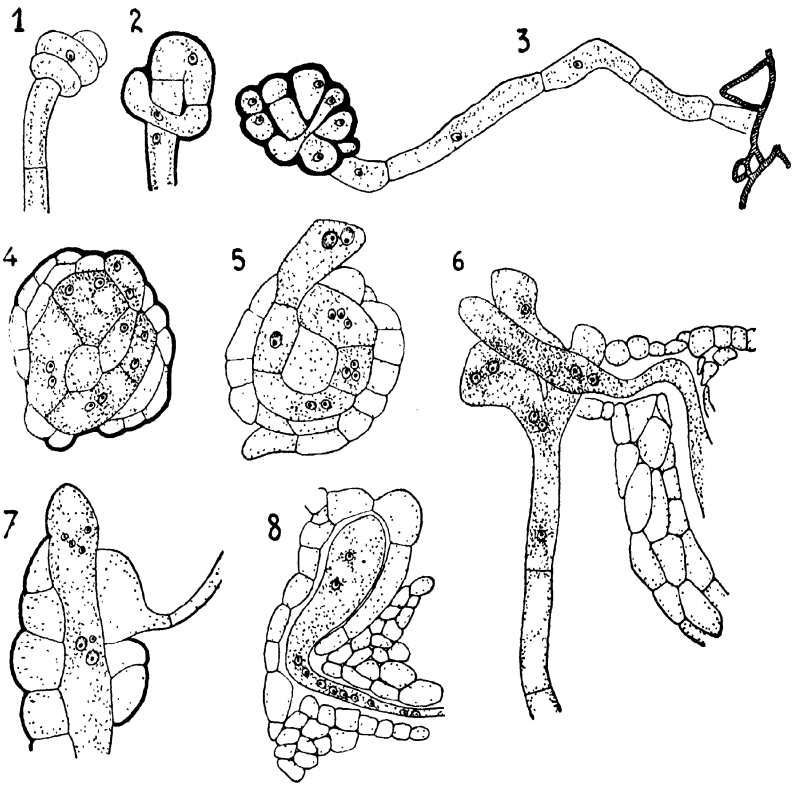


FIG. 180.—*Venturia inaequalis*. Development of perithecia. 1, 2. Helical hyphae. 3. Section through primordium of perithecium, still showing its development from helical hyphae. 4. Somewhat older stage, the ascogonium already divided into several cells. 5. The same, the terminal cell beginning to develop as a trichogyne. 6. The antheridium is surrounding the trichogyne at the right. 7. Section through a trichogyne fusing with an antheridium. 8. Section of trichogyne after nuclear migration, the male nuclei already at the lower end of the trichogyne. (× 580; *after Killian*, 1917.)

In this second saprophytic phase the formation of perithecia begins. Here and there a remaining hyphal branch, which is not further differentiated from a purely vegetative hypha, coils to a helix (Fig. 180, 1); at first it is aseptate, then separated into binucleate cells. The cells of the helix lie close together in a plectenchymatic knot, with the peripheral cell walls much thickened (Fig. 180, 2). The helical arrangement is

gradually lost. The uninucleate thick-walled peripheral cells of the knot elongate and serve as the future one-layered peridial wall, while the thin-walled inner cells still remain isodiametric and multinucleate. One of the latter grows gradually to a large vermiform cell. It begins to divide

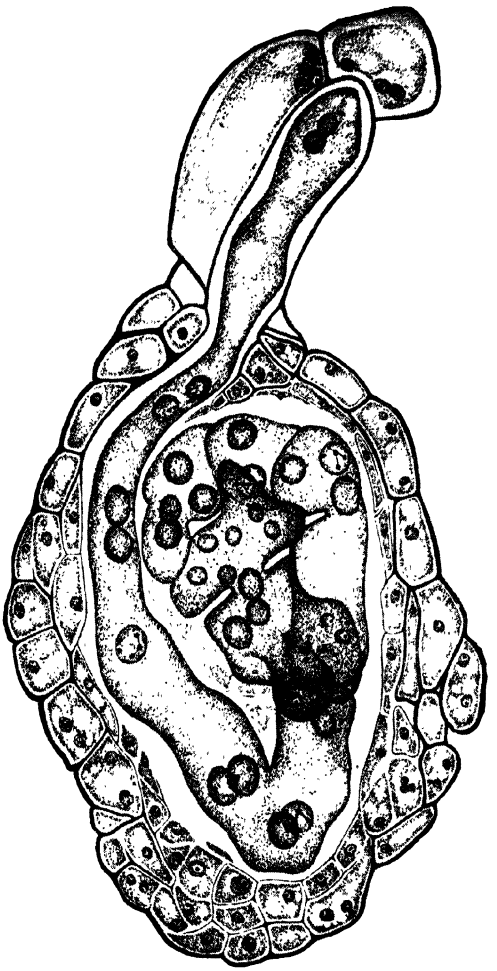


FIG. 181.—*Venturia inaequalis*. Diagrammatic section of fertilized ascogonium. The septa have dissolved, the nuclei are migrating to the inner cells. (× 875; *after Killian*, 1917.)

and produces a (at most a 7-membered) chain of more or less isodiametric, bi- to quadri-nucleate cells, the future ascogonium (Fig. 180, 4). The peripheral terminal cell of the ascogonium swells clavately, later elongates and forms the future trichogyne (Fig. 180, 5).

Meanwhile an antheridium arises on or near the ascogonial mass, from the branch of a hypha which is not differentiated from the usual vegetative hyphae. Later, its tip thickens, the terminal cell completes many nuclear divisions and forms several (usually about three) lobate projections (Fig. 180, 6) into which the nuclei migrate (mostly in pairs, seldom 4 to 8).

The trichogyne grows actively toward the antheridium. Thus in Fig. 180, 6, at the exit of the perithecium, it changes its direction of growth

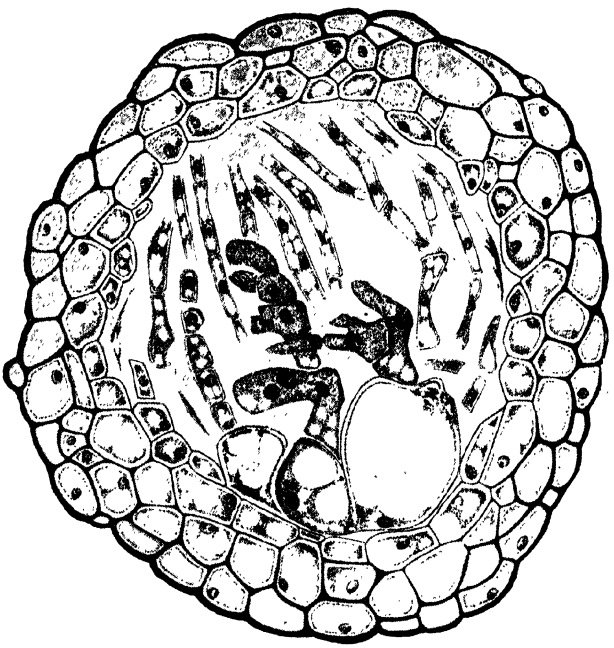


FIG. 182.—*Venturia inaequalis*. Section through perithecium with young ascogenous hyphae and paraphyses. The three large cells are empty ascogonial cells from which the ascogenous hyphae grow. (× 875; *after Killian*, 1917.)

and, bending at a sharp angle, grows toward the antheridium at the left. These cell processes surround the trichogyne, like the fingers of a hand. By contact, the antheridium is stimulated to further development. Its cells and nuclei multiply and enlarge and the recently formed sprouts again clasp the lower portions of the trichogyne, so that the coils cover it (Fig. 180, 7).

When both organs are firmly united, a pore forms and the male nuclei enter the trichogyne. Probably not only the nuclei in the copulating antheridial branch enter, but also the others, since at the end of migration all the antheridial branches seem empty. The male nuclei migrate to the lower portion of the trichogyne (Fig. 180, 8). Neither of the tricho-

gyne nuclei takes part in this migration; they appear to have fulfilled their function and soon degenerate together with the trichogyne and antheridium.

The septa of the ascogonium are successively dissolved. The male nuclei, thus, have unhindered access to the ascogonium itself and fuse with the female nuclei. The middle portion of the ascogonium elongates, assumes an irregular lobate appearance (Fig. 181) and grows in the spring to ascogenous hyphae.

Meanwhile the wall of the perithecium becomes three- to four-layered. Uninucleate paraphyses grow from the cells of the inner wall layer, separate the perithecium from the remains of the ascogonium and make space for the penetrating asci (Fig. 182). At maturity, the ascospores may be shot up as much as 1.5 cm. The meaning of this ontogeny will be clear only when more species of the Sphaeriales have been studied cytologically; still there can be no doubt that the *Venturia* type is connected directly to that of the Plectascales.

Gnomoniaceae.—This second family with immersed perithecia in the non-stromatic Sphaeriales has been thoroughly studied in culture by Klebahn (1905 to 1918). *Gnomonia veneta* (*Apiognomonia veneta*) on *Platanus*, causes characteristic brown spots, following the veins of leaves, in spring until the middle of June. About the end of June, the spots develop brown or black, warty acervuli of *Gloeosporium nervisequum* on the upper surface of the leaf, usually only along the veins. Later the same sort of acervuli erupt from the petiole; as they remain there a long time, covered by the epidermis, the dimensions of their acervuli and conidia are smaller. Therefore they were earlier described as a distinct species, *Gloeosporium Platani*.

Besides the brown spots on the leaves, *G. nervisequum* produces a sudden wilt of the young shoots. Numerous conidial sori, earlier described as *Discula Platani* (*Myxosporium valsoideum*) are formed in the cork tissues with conidia like those of *G. nervisequum* (Fig. 183, *d*); Klebahn proved experimentally their position in this developmental cycle. In late autumn and winter black structures with peculiar conidia arise under the epidermis of the dead leaves, raise and rupture it by their growth (Fig. 183, *c*); this form was originally described as *Sporonema Platani* and *Fusicoccum veronense*. When the fallen leaves have overwintered, the perithecia of *Gnomonia veneta* are formed. These are nearly spherical with a short beak (a characteristic feature of the Gnomoniaceae, Fig. 183, *a*). Normally they are completely immersed in the dead leaf tissue with the beak reaching the upper surface of the leaf or projecting slightly above it. The wall consists of about four layers of cells with brown walls.

The asci are clavate, with a thickened tip provided with a pore. The hyaline, two-celled ascospores germinate in nutritive solutions to a

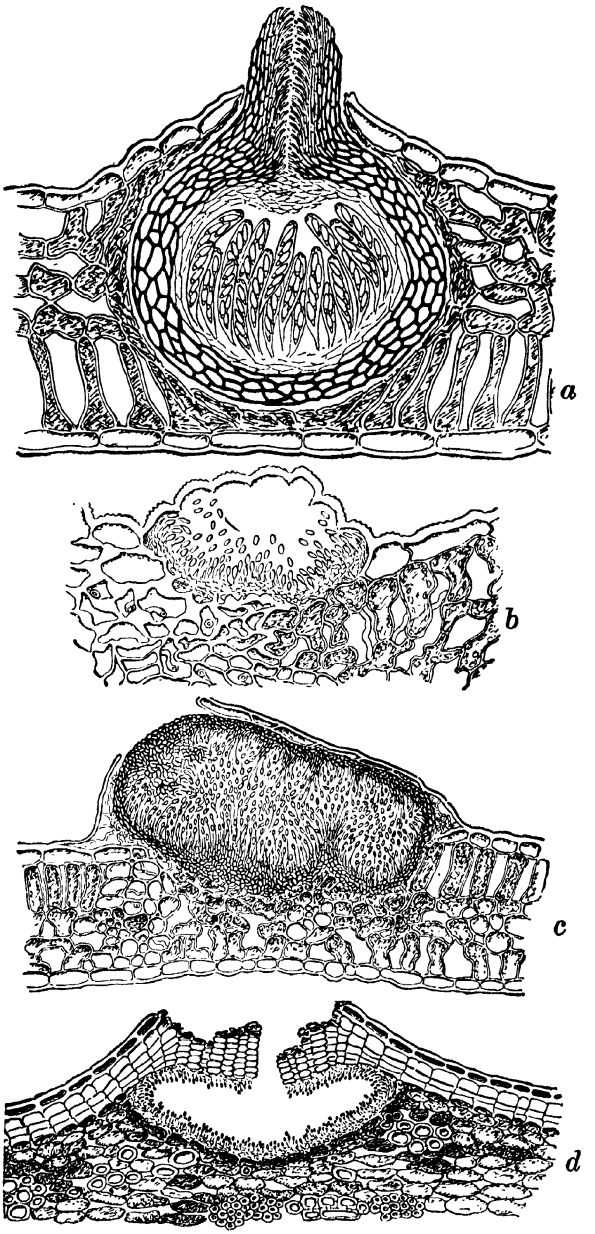


FIG. 183.—*Gnomonia veneta*. *a*, Perithecium. Secondary spore forms. *Gloeosporium nervisequum*, *b*, on living leaves. *Sporonema Platani*, *c*, on rotting leaves. *Discula platani*, *d*, in bark under the lenticels. (*a* × 250; *b* × 260; *c* × 160; *d* × 85; *after Klebahn*, 1905.).

slender mycelium which cuts off oval conidia, either laterally or terminally, and on certain media, develop fructifications similar to those of *Sporonema Platani*. On other media they form the pycnia of *Discula Platani* and later the fundaments of the perithecia of *Gnomonia veneta*.

Therefore, the conidia of *G. veneta* may arise in not less than four different types, three on the hyphae, which so far have only been observed in pure cultures, then on leaves, without pycnia (*Gloeosporium nervisequum*) on branches in sori with less marked pycnia (*Discula Platani*) and finally in dead leaves in black, occasionally many chambered pycnia (*Sporonema Platani*). If one considers the scattered mycological publications and the tendency of some authors to describe imperfect stages, it is not surprising that *G. veneta* has 15 synonyms in the literature.

The imperfect forms of other pathogenic species show a polymorphism similar to that of *G. veneta*. *G. erythrostoma* (*Apiognomonia erythrostoma*) a leaf spot of cherry, forms pycnia out of which the conidial mass is pressed as a helical thread. Solitary, helical, multinucleate ascogonia develop and fuse with a small antheridium. Nuclear migration occurs and the ascogenous hyphae of the hook type develop in the normal manner (Brooks, 1910; Likhité, 1926).

Gnomonia leptostyla, the anthracnose of walnuts, has only free conidiophores which sometimes in the same sorus, but more often separately, cut off at the pointed end, fusarioid macroconidia (*Marssonina Juglandis*) and smaller, unicellular bacilliform microconidia (*Leptothyrium Juglandis*). The young antheridia and ascogonia develop in the degenerate parenchyma. The antheridia are unicellular and multinucleate. They fuse with the ascogonia and degenerate, while the ascogonia continue to develop, putting forth on all sides, short protuberances from which the asci develop directly, as in the *Plicaria succosa* type (Likhité, 1926).

Ophiobolus has long slender ascospores which often separate into their individual cells. Its best-known species is *O. cariceti* (*O. graminis*, *O. herpotrichus*), the cause of take-all of wheat and other cereals (Kirby, 1924). Imperfect forms have not yet been reported. The mycelium is uninucleate and intracellular, capable of penetrating cells without developing haustoria. At the beginning of spermagonial formation, the tips of a number of hyphae congregate and, by further growth and intertwining, form a loose ball of hyphae. This expands and the outer layer becomes increasingly pseudoparenchymatous. The cavity is bounded by a layer of uninucleate, pyriform cells with their narrow ends toward the center of the cavity. They give rise to short, narrow cells of varying length which abstrict the bacilliform spermatia from their tips. The spermatia are sometimes arranged in short chains but are no longer functional. Their nuclei are very large and they are completely devoid of reserve material.

While the spermagonia are developing, the mycelium forms small coils which produce a number of archicarps, each furnished with a trichogyne. Subsequent development shows these structures to be abortive. Perithecial development proceeds from vegetative hyphae which intrude into the space bounded by an ascogonial coil which remains for a considerable time during development. The ascogenous hyphae develop apogamously. Apparently the process is begun by the conjugation of two or more vegetative cells. The nuclei of the ascogenous hyphae are usually in pairs and the cytology of the ascus is normal. Meiosis occurs at the first ascus division. The ascospores are divided into six uninucleate cells (Jones, 1926). Kirby (1923) suggests that this species is heterothallic, but Davis (1925) working with Kirby's cultures, was unable to confirm this report.

Glomerella, also important in plant pathology, is characterized by perithecia united into stromata, otherwise it is like *Gnomonia*. In the United States, various biological strains of *G. rufomaculans* (*G. cingulata*) attack the bast and fruits of numerous orchard trees and the grape. Its imperfect stage is *Gloeosporium fructigenum*. There seems to be a slight heterothallism, since single spore mycelia form abnormal perithecia with difficulty. When the complementary mycelium is added, normal perithecia are formed freely (Edgerton, 1914).

While the Mycosphaerellaceae and Gnomoniaceae are characterized among the Sphaeriales having immersed perithecia, by the perithecia being solitary or, very rarely, united into stromata, as in some species of *Mycosphaerella* and *Glomerella*, in the last three families of the Sphaeriales to be discussed here, the Diatrypaceae, Diaporthaceae and the Xylariaceae are distinguished by the immersion of their perithecia in a stromatic plectenchyma. The two former are related to the Xylariaceae somewhat as *Nectria* to the *Mycomalus–Ascopolyporus* stage; they chiefly include simple stromatic forms on bark whose stromata are only slightly raised from the substrate, while the Xylariaceae develop fully individualized fructifications independent of the substrate.

Diatrypaceae.—This family, called the Allantosphaeriaceae by Hoehnel in his later treatment, is characterized by more or less colored, mostly unicellular spores. The asci are 8 or many spored, clavate, often with a thickened tip, long, stipitate and arranged in a hymenium lining the base and sides of the perithecium. Paraphyses are usually present, gelifying in age. The ostioles are sulcate.

The simplest forms are shown by *Eutypa Acharii*, *E. lata* and *E. spinosa* on decorticated wood. The perithecia of these species are scattered singly but are united by a blackened crust on the surface of the substratum. A primitive hyphomycetous stage is retained but conidial locules are formed in a stroma.

The first advance from these forms is the production of a rich mycelium about the fructifications, within the substratum. This soon results in the development of a differentiated entostromatic area bounded by a blackened marginal zone. From this stage we may discern four developmental series.

The first series includes the species of *Diatrype* with an effused or isolated stroma. It is characterized by the formation of a strongly developed, deciduous ectostroma, which throws off the periderm from the entire surface of the equally well-developed entostroma, whose darkened surface layers then form the widely erumpent disc. This development of entostroma gives a distinct and abrupt margin to the erumpent stroma. The perithecia are arranged parallel to one another in a single layer; they have short stout necks and are separately erumpent through the encrusted surface of the entostroma as sulcate, disciform ostioles. The conidia are always formed from ectostromatic tissue, and are long filiform, unicellular, curved and hyaline.

In *Diatrype stigma*, the perithecia are imbedded in a strongly differentiated entostroma, bounded by a blackened marginal zone. On the surface of the bark there is early developed an effused layer of ectostroma which swells rapidly at maturity and throws off the periderm over large areas. This exposes the developing entostroma whose surface is then rapidly blackened, forming an erumpent disc. The young ectostroma increases greatly in thickness at various points and in these cushions of tissue, labyrinthiform conidial locules are formed (Fuisting, 1867; Wehmeyer, 1926).

In *D. tremellophora* (Wehmeyer, 1926) and *D. disciformis* (Ruhland, 1900) the ectostroma is thrown off by the developing entostroma.

Diatrype disciformis is at first parasitic, then saprophytic on stems and twigs of beech, rarely on other frondose woods. Between the bark parenchyma and the periderm, the hyphae intertwine into a flat disc which gradually curves in the middle into a blunt head, the later ectostroma (epistroma of Fuisting, 1867) (Fig. 184, 1). On account of its harder consistency and rapid growth it exerts such a pressure on the periderm that it raises it in the form of flat pustules from the bark parenchyma. Around the base of the head, there develops a flat cavity into which the conidiophores grow from the disc parenchyma and cut off an enormous number of small much-twisted hyaline conidia, which are flesh red in mass (Fig. 184, 2).

The cap itself remains sterile. By its elongation the periderm is ruptured and the conidia are liberated through the tear. Gradually the abscission ceases and the hyphae are retained as the ground tissue of paraplectenchyma. The hyphae of the cap, which by the rupture of the periderm are exposed to the air, begin to swell, turn brown and gradually

die. At the same time the head again grows upward from below, by a meristematic layer at its base, 8 or 9 cell layers thick.

Meanwhile the plectenchymatic fungus tissue has spread into the bark parenchyma lying under the plectenchyma disk. There it forces the cell elements apart and, by gradual resorption of their bark cells, forms a comparatively thick plectenchyma, the later entostroma (hypostroma, Fuisting, 1867). In it the perithecia are formed nearly on a level within the spherical hyphal knots. In each lies an ascogonium without trich-

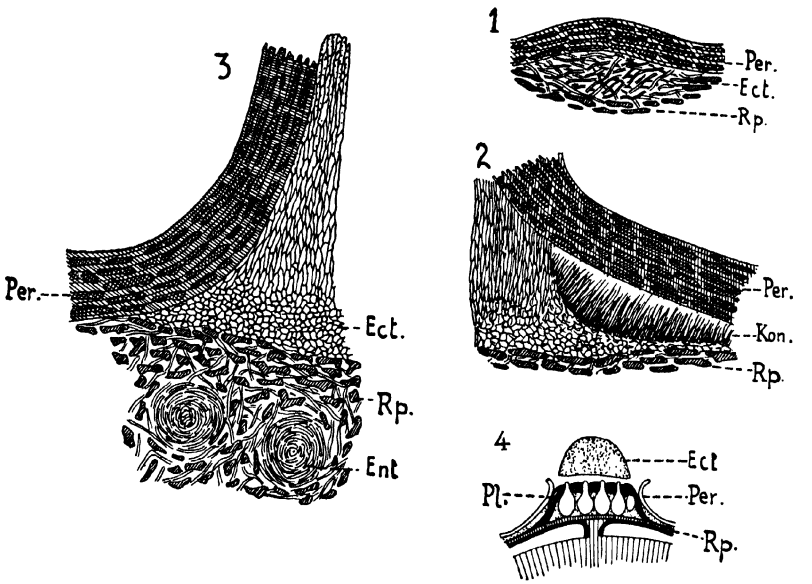


FIG. 184.—*Diatrype disciformis*. 1. Section of fundament of ectostroma. Above the peridium, *Per;* in the middle ectostroma, *Ect*, and below the bark parenchyma, *Rp*. 2. Older stage. The central portion of the ectostroma is already verruciform while the peripheral portion (right) is still forming conidia. *Kon*, conidial stroma. 3. Section through ectostroma and entostroma, the latter has already formed perithecia. 4. Diagrammatic section through a mature fructification. The ectostroma, *Ect*, has already separated; *Pl*, placodium. (1, 3 × 400, 2 × 270; *after Ruhland*, 1900.)

ogyne (Fig. 184, 3), from which the ascogenous hyphae are formed in an unknown manner.

The distal outer layer of the entostroma subsequently changes into a horny sclerotic rind which is only interrupted by the perithecial necks. Thereby the connection with the ectostroma is loosened, the latter is thrown off, and the mature perithecial entostroma lies free in the ruptured periderm. This horny, sclerotic rind layer, surrounding the perithecial mouths, is called a shield or **placodium** (Fig. 184, 4).

One of the causes of great confusion in the systematic literature of the Sphaeriales is that the development of the stroma in the higher forms

as here outlined occurs only under very favorable conditions. With the sudden appearance of drought, development may be stopped at the stage of Fig. 184, 1 or 2, and the observer would then find under the periderm only a sterile sclerotial plectenchyma, possibly with the remains of the conidial stage. The distinction between ectostroma and entostroma, perhaps through greater resistance of the periderm or by unfavorable growth conditions in the bark parenchyma, can be so disturbed that the definite parts which form only perithecia or only conidia can no longer be distinguished. Or the perithecia may arise under each other in several layers. The figures given here represent only the simplest case.

The second developmental series is characterized by the polysporous asci and presents a type of development intermediate between that of *Diatrype* and *Eutypella*. The structure of the entostroma is that of the *Eutypella* series, but the conidial stage is usually ectostromatic. It may be conceived as beginning in forms like *Quaternaria Persoonii*, in which the perithecia are in groups of two to four within the upper bark tissues. The lower bark tissues and the surface of the wood are blackened. Entostromatic mycelium develops about the perithecial groups, giving them a pustulate appearance. This mycelium often develops over extensive areas, forming an effused, pustulate stroma, often bounded beneath by a definite blackened zone. The stroma develops numerous clusters of perithecia which are collectively erumpent through a small ectostromatic disc. The grouping of the perithecia occurs before the entostroma is differentiated, while it still forms effused patches (Wehmeyer, 1923). This species shows a stromatic structure intermediate between *Eutypa* and *Eutypella*, but with a conidial stage similar to that of *Diatrype*.

An unnamed species of *Cryptovalsa* on *Cercis canadensis*, reported by Wehmeyer (1926), is a very primitive form. The perithecia, occurring in pairs or singly, arise in the bark tissues but become partially or even wholly sunken in the wood at maturity. Just above the perithecial initials, there is a blackening of the bark tissues where some of the hyphae penetrate the periderm and weaken it, thus enabling the growing perithecial necks to penetrate. The blackened zone extends down to the wood surface, where it spreads out between the perithecia. There is very little entostromatic development and no ectostroma except the blackened zone. *Cryptovalsa sparsa* is at about the stage of development of *Quaternaria Persoonii*.

In *Cryptovalsa Nitschkei*, the entostroma is more highly developed. The entostromatic areas are usually effused and contain a number of perithecial clusters, although isolated stromata occasionally occur with only one group of perithecia. Ordinarily the ectostroma is little developed, but in culture, they produced yellow, erumpent ectostromata containing labyrinthiform locules bearing conidia. The entostromatic

mycelium often develops in the surface layers of bark cells just beneath the ectostroma, and fuses with it, giving the appearance of an ectostroma partially sunken in the bark. Such a fusion and consequent extension of conidial locules into the entostromatic portion of this tissue, is characteristic of this series.

In *Diatrypella quercina*, the greenish yellow ectostroma develops above the perithecia. In *D. Frostii* the isolated entostromatic areas ordinarily contain a single group of perithecia. *Diatrypella betulina* represents the highest stage of the series. The widely erumpent blackish disc contains separately erumpent, quadrisulcate, disc-like ostioles. The disc tissue consists entirely of yellowish green fungus tissue with a blackened surface crust. It originates upon the bark surface beneath the periderm and is ectostromatic. The ectostroma is not deciduous but forms the erumpent disc itself. The perithecia arise within a hyaline entostroma, increase enormously in diameter and push up the ectostroma.

The third series stage is found in *Eutypella* and is characterized by the 8-spored asci, the small but distinct ectostroma with the conidial locules formed in the entostromatic tissue of the bark. The species vary from those with an effused entostroma to those with definitely isolated stromata. *Eutypella tumida* shows this whole range of variation in a single species.

In the fourth series, which is more heterogeneous, the stromatic development occurs mostly in the entostroma with a great reduction of the ectostroma. The spores have a tendency to become dark brown, straight cylindrical and uniseriate; the asci become cylindrical and shorter stalked, with an increase in the filiform hyaline paraphyses. Species of *Cryptosphaeria*, *Valsaria* and *Anthostoma* illustrate these tendencies.

Diaporthaceae.—In this family the asci have no definite stalks and do not remain in a definite hymenial layer after maturity. When moistened, the base of the ascus contracts and dissolves, pinching off the ascus from its attachment. The ascus walls are delicate and break down in water. As a result, the entire central cavity of the perithecium becomes filled with a mass of free asci and spores. The paraphyses which are numerous in young perithecia are evanescent. In the higher forms they are more numerous and persistent in mature perithecia. Most species have two types of conidia.

The first series includes *Diaporthe*, *Melanconis* and *Pseudovalsa*. There is a general tendency toward the development of a stroma and the clustering of perithecia. In *Diaporthe* the spores remain hyaline, in *Melanconis* they become brown in the higher forms, in *Pseudovalsa* they become brown and multicellular. In *Diaporthe* the conidia are hyaline, unicellular within pycnia; in *Melanconis* the conidia become brown, unicellular, and the conidial layers more exposed; in *Pseudovalsa* they become brown and septate.

The origin of *Diaporthe* from *Gnomonia* is very evident. In the simpler species the transition is very gradual. The compound fructifications have arisen from the clustering of perithecia and the development of a light-colored, differentiated entostroma circumscribed by a dark marginal zone. The imperfect forms consist of a *Phomopsis* type of fructification with an enclosed locule formed in an ectostroma which is intimately associated with the entostroma beneath, when that tissue is well developed.

In *Diaporthe leiphaemia*, which occurs on damp fallen oak twigs (Fig. 185, 1) between periderm and bark parenchyma, the hyphae intertwine to a narrow plectenchymatic covering, the fundament of the ectostroma; this develops outwards to a verucose head and thereby accomplishes the

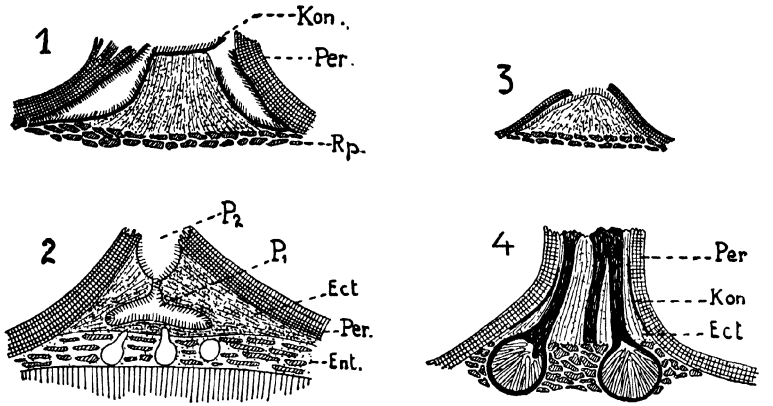


FIG. 185.—*Diaporthe leiphaemia*. 1. Section of old pycnium. *Diaporthe syngenesia*. 2. Section of old pycnium. P_1, original pycnium with large conidia; P_2, secondary pseudopycnium with smaller conidia. *Melanconis stilbostoma*. 3. Section of young ectostroma, bearing conidia. 4. Diagrammatic section of mature fructification. *Kon*, shows the remnants of conidial layer between periderm and stromatal surface. *Ect*, ectostroma; *Ent*, entostroma; *Per*, periderm; *Rp*, bark parenchyma. (*After Ruhland*, 1900.)

opening of the periderm. Hereupon it is differentiated within to a large pycnium whose interior is entirely covered with conidiophores cutting off hyaline bacilliform conidia. Subsequently at the middle of the base of the pycnium, conidial formation stops and the ectostroma which lies there develops to a comparatively high plectenchymatic cylinder which projects into the cavity of the pycnium and divides lengthwise into two special sinuses. *Diaporthe oxyspora* (Wehmeyer, 1928) agrees with this type of development, having a *Phomopsis* conidial stage.

In *Diaporthe syngenesia* (*D. Berlesiana*), the conidial hymenium is more elaborate. The ectostromatal layer, which separates pycnium from periderm, is much more developed than in *D. leiphaemia*. After the periderm is ruptured, conidial formation overlaps to the face of the distal ectostromatic layer (Fig. 185, 2) and thereby forms on the outer

side of the opening of the original pycnium p_1 a second external false pycnium p_2. The pycniospores of the former are larger and thicker than those cut off on the upper surface. The stromata develop further as in *Diatrype disciformis*. First an entostroma is laid down which serves as the site of perithecial formation. In contrast to *D. disciformis*, however, the upper part of the entostroma is not differentiated into marked sclerenchymatic placodium, so that the connection of both stromatal layers is not so roughly interrupted. The perithecial necks gradually push out through the ectostroma and help to raise the dark brown layer which has meanwhile died. Finally all the stromatal substance blackens. Whether sexual acts occur in the perithecia is not yet determined histologically; possibly they are present, as in certain strains of *Diaporthe perniciosa* there is a peculiar physiological sexual differentiation (Cayley, 1923).

Apioporthe anomala has a strongly developed stroma, like that of *Diatrype*, and unequal two-celled spores. *Apioporthe obscura* has a well-developed stroma about the perithecia, although it is not as erumpent as in *A. anomala*. In *A. phomospora*, this entostromatic development shows a still greater reduction, with only a slight development of mycelium about the perithecia and a slight blackening of the bark surfaces above them. Conidia are produced in stromata by the breaking up of the mycelium (Wehmeyer, 1928).

Parallel to the *Diaporthe* group, we find a second sub-series which does not produce a dark marginal zone, at least not until late in the history of its development. In *Melanconis* the stromatic development is limited to an ectostromatic disc and the perithecia are imbedded in the unaltered cortex. The ascospores become colored and uniseriate in the ascus, but remain two-celled. The imperfect stage is a typical *Melanconium* with the conidia borne in the shallow cavities on the sides of a sterile disc, or over the entire surface of a hemispherical ectostroma.

Melanconis stilbostoma is fairly common on the dry twigs and pieces of stem of *Betula alba*. Under the periderm, it forms a fibrous cell complex which arches out to a head (Fig. 185, 3) and cuts off over its whole surface, dark-walled conidia of *Melanconium bicolor*. On account of the formation of conidia on flat or pulvinate layers, *Melanconis* is usually regarded as the type of the Melanconideae and hence contrasted to the Valsaceae in the narrower sense, which form conidia in pycnia. Frequently the fungus, especially in unfavorable weather, does not attain this conidial stage, but transforms its pseudoparenchyma into a sclerotic tissue.

In contrast to the previous genera, the entostroma remains mycelial and does not develop to an independent stromatal layer. The necks of the perithecia grow through the whole ectostroma, whose outer layer changes into a rind-like placodium (Fig. 185, 4). While in *Diatrype* the

placodium belonged to the entostroma, here it is supplied by the ectostroma; hence the first genus is called entoplacodial, the latter ectoplacodial.

In *Pseudovalsa* there is no definite ectostroma and where a stromatic mycelium is formed, it is within the bark about the perithecial necks. Where the entostroma develops, there is a faint, dark, marginal zone, but the entostromatic mycelium is usually dark colored, hence the stromatic areas are not light as in *Diaporthe*. The imperfect stage is ectostromatic, but is usually not connected with the perithecial stroma, or where it is, as in some species of *Pseudovalsa*, the ectostroma is reduced.

Diaporthe Wibbei, var. *Comptoniae* on *Myrica asplenifolia*, forms a transition from *Diaporthe* to *Pseudovalsa*, showing no marginal zones in the substrate, and producing septate, appendiculate conidia. In the stromatic tissue, loose ends of hyphae appear at one or several points and cut off conidia until a central, spherical or irregular cavity with a peripheral hymenium of conidiophores results. The subhymenium acts as a nurse tissue to the conidiophores. The connection of conidium and conidiophore becomes constricted and elongate. The conidium is abjointed at the apex of this elongate tip. The next conidium is constricted somewhat back of the apex of the conidiophore. The growth of the portion of the conidiophore above this constriction gives rise to the spore while the elongation of the stalk of the previous conidium forms the apical appendage. This conidial stage was described as *Pestalotia flagellifera* (*Barclayella flagellifera*, *Neobarclaya flagellifera*). The perithecial stroma lacks an ectostroma and the blackened zones, while the entostromatic hyphae develop about the perithecia, suggesting the simpler species of *Pseudovalsa* (Wehmeyer, 1928).

In *Pseudovalsa lanciformis* on dead branches of *Betula alba*, the entostroma is entirely absent. The hyphae connect inside the bark into a tangled stroma which at first cuts off conidia on its surface (*Coryneum disciforme*), then ruptures the periderm and forms ascogonia and perithecia.

In the second series, the main line of development in *Cryptosporella* and *Cryptospora* shows a similar stromatic structure and similar imperfect stage. The relationships among the lower forms are still vague. *Gnomoniella* has no stromatic development and may be considered as an ancestral form. *Sphaerognomonia* shows the development of a stromatic "clypeus" about the ostiole while *Mamianiella* shows a well-developed stroma about the perithecium. These three genera are found on leaves. *Mazzantia* (Hoehnel, 1918) has a stromatic structure identical with that of a well-developed *Diaporthe*, but it has unicellular ascospores. *M. Gallii* has a well-developed, differentiated entostroma within the tissue of the substrate, bounded by a darkened zone. The cylindrical, hyaline conidia are borne in an enclosed locule within the stroma.

The species of *Cryptosporella* and *Cryptospora* are characterized by unicellular ascospores and by a conical ectostromatic disc about which the perithecia are arranged circinately with the unaltered bark cortex. There is no differentiated entostromatic area nor dark marginal zone. The imperfect stages have been placed in *Fusicoccum* and *Disculina* (*Cryptosporium*). The fructifications consist of an ectostromatic cushion which contains open cavities or enclosed locules, usually on the marginal portions of the ectostroma. The conidia are unicellular, hyaline and more or less elongate. These characters show a relationship to *Melanconis*.

The third series includes *Valsa*, *Leucostoma*, *Valsella*, *Endothia* and *Valsaria*. In *Valsa* the structure is quite simple and resembles that of *Melanconis*, but in the other genera there is a well-developed and strongly differentiated entostroma. Ascospores, except in some species of *Endothia* and *Valsaria*, are allantoid, hyaline and unicellular. The conidial chambers are numerous or labyrinthiform and produced both in entostroma and ectostroma. *Glomerella*, with its allantoid ascospores, presents a possible origin for this series among the simple Sphaeriales. There seems to be a wide gap between such forms and the species of *Valsa*.

The species of *Valsa* have a definitely differentiated truncate conical ectostroma which forms the erumpent disc. The perithecia are buried in the bark cortex beneath this ectostroma. The entostroma is very slightly developed and visible only under a microscope, while the ectostroma is sharply defined. The imperfect stage belongs to the form genus *Cytospora*. The fructifications consist of an entostroma containing numerous locules which often coalesce into a labyrinthiform chamber. The conidia are small, allantoid, unicellular, hyaline and ejected in large numbers in the form of a spore horn.

In *Leucostoma*, the differentiation between ectostroma and entostroma is vague. In some species, as *Leucostoma subclypeata* (*Valsa subclypeata*), there is formed a differentiated cap of ectostromatic mycelium. In all species the stromatic area is delimited very early in its development by a dark marginal zone of tissue which limits the size of the stroma. In *Leucostoma Persoonii* (*Valsa leucostoma*), the dieback of stone fruits, this zone runs just beneath the periderm and the stroma develops between the periderm and the bark surface. In *Leucostoma subclypeata*, this blackened zone may penetrate into the bark, cutting off a spherical area within which the bark cells are absorbed and replaced by a stromatic fungous tissue. Where there is formed a differentiated cap of tissue which opens the periderm, the stromatic tissue, in which the perithecia are imbedded, should undoubtedly be considered as entostroma. In many cases this tissue develops entirely upon the bark surface.

Valsella differs only in its polysporous asci. *Endothia* is also close to *Leucostoma*. In *E. parasitica* (Fig. 186) the stroma usually arises as a

hyaline ectostromatic cushion just beneath the periderm. The amount of this tissue formed varies widely. When a well-developed ectostroma is formed, pycnidia are formed within it. If this tissue is much reduced it remains sterile and, unless pycnia are formed in the entostroma, only perithecia are produced. At about the time the ectostroma ruptures the periderm, its tissues are colored yellow becoming a reddish orange. The perithecial initials are formed within the bark cortex beneath the ectostroma. Along with the development of the perithecia, there is production of entostromatic mycelium. This may be so vigorous that a large stromatic mass containing only the remnants of the bark cells is pushed up through the periderm. In these larger stromata the ectostroma can no longer be distinguished (P. J. Anderson, 1913). This species has done much damage to *Castanea* in the United States and Eastern Asia (Shear, Stevens and Tiller, 1917). *Endothia gyrosa* and *E. singularis* show a great growth of entostroma, resulting in a large crumbly mass of fungus tissue in which only the remnants of the bark cells may be found. This genus must have arisen as a divergent line from some ancestor of *Valsa* and *Leucostoma* rather than directly from the latter.

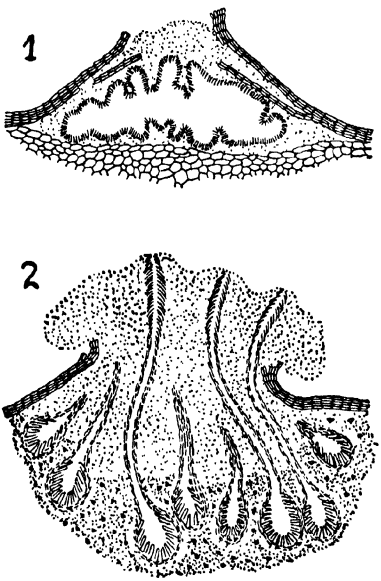


FIG. 186.—*Endothia parasitica*. 1. Section of pycnium. 2. Section of perithecial stroma. (*After Heald*, 1913.)

Xylariaceae.—The haplostromatic type is most marked in the last family (Tavel, 1892; Theissen, 1909). The simpler genera, as *Nummularia*, are directly connected to the Diatrypaceae and Diaporthaceae. They form round, discoid, generally amorphous, crustose black stromata, as *N. Bulliardi* on beech branches. Their mycelia in cultures have branched, fibrous conidiophores with heads of colorless spores. In the interior of the young hypophloedal stroma, there arises in a simple cavity, a flat conidial hymenium which cuts off similar conidia. The outer layer of the stroma covering it is pushed off with the periderm of the twig, so that at maturity the stromata of the perithecia lie free on the surface.

In the other genera, the stromata develop wholly on the surface of the substrate but as in *Ustulina*, are indefinite in form. *U. vulgaris* covers the surface of old trunks and stems of frondose woods with often gigantic, undulating black crusts which in youth are soft and covered by

a conidial hymenium but later become brittle, hard and carbonaceous. A related species, *U. zonata*, causes a root disease of *Hevea* and tea.

In the higher genera these external stromata, as in the higher Hypocreales, gradually attain characteristic limits and become true fructifications. At first they arch in the middle and become hemispherical or (as in *Mycocitrus* and its relatives) tuberous, *e.g.*, in *Hypoxylon* (Fig. 187) and *Daldinia;* but one may not draw a sharp line between these two genera and *Ustulina* as their stromata, especially in immature specimens, often still remain resupinate crusts. The mycelia of both these genera exhibit very beautiful, graceful, often characteristically branched conidiophores whose spores in *Hypoxylon unitum* are lateral on the conidiophores and in *H. fuscum* and *H. coccineum* are terminal in a solid little head.

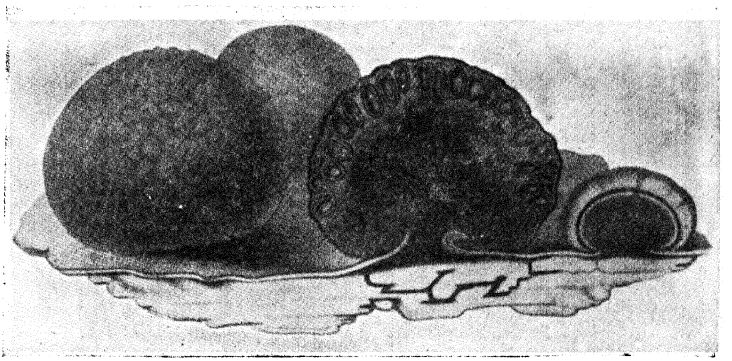


FIG. 187.—*Hypoxylon coccineum.* Fructifications in various stages of development, the youngest still bearing conidia. (*After Tulasne.*)

Coremia also occur. Usually the conidiophores are scattered over the whole mycelium; more rarely their appearance is limited to the surface of the young stroma. They are always present there, however, and by the mass of their spores give it a powdery appearance and a peculiar color often differing from that of the mature fructification. In all cases the perithecia develop after the disappearance of the conidial fructification. Both genera inhabit, mainly, rotting wood and dry branches. In *Hypoxylon* the stromata are homogeneous, in *Daldinia* in concentric layers; this distinction is rather quantitative, however, and only reliable in extreme forms; thus the tropical *D. exsurgens* shows a slight zonation but is otherwise similar to *Hypoxylon.*

In the highest genera, as *Xylaria, Thamnomyces* and *Poronia,* as in the highest Hypocreales, there begins the differentiation of the stromata into a sterile and fertile part. *Xylaria* is cosmopolitan, but especially well represented in the tropics. It generally inhabits dead wood, rarely dung

or dry fruits (as *X. carpophila* on beechnuts). From the ascospores develops an extended mycelium whose hyphae unite into thick strands; these grow tall and show an intense heliotropism so that even when under bark or tree trunks they easily come to the outer surface. They are first differentiated into a black pseudoparenchymatic rind and a light fibrous core and then gradually develop to the cylindrical, clavate or branched fructifications. Many species (inconvenient for systematists!) are inseparable

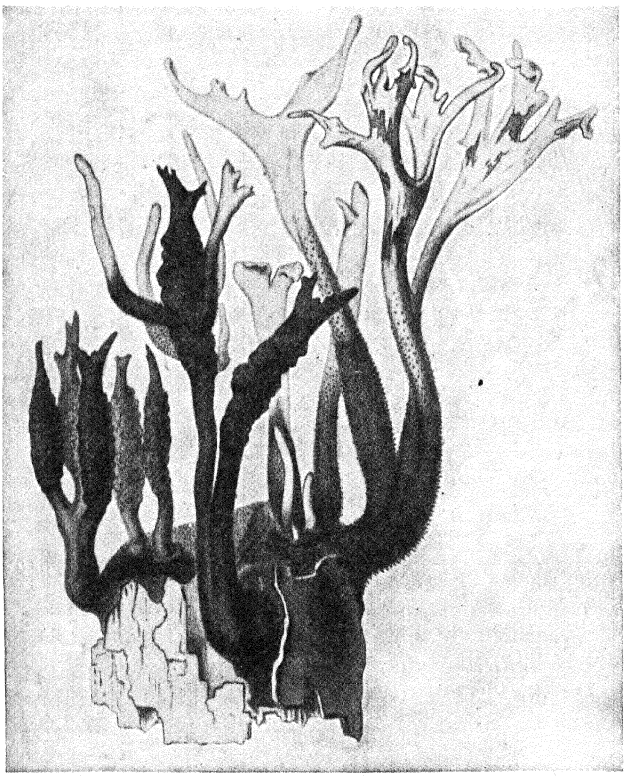


FIG. 188.—*Xylaria Hypoxylon.* Group of stromata on fallen wood. (*After Tulasne.*

from *Hypoxylon*, thus *X. obovata*, *X. anisopleura* and *X. allantoidea* show in the same species all sorts of transitional forms from Hypoxyloid central attachments to Xylarioid stipes. In spite of its inconspicuous occurrence in nature, its formation in culture is dependent on conditions of nutrition; thus *X. Hypoxylon* requires asparagin as a nitrogen source in formation of fructifications, while *X. arbuscula* and *X. polymorpha* require ammonium nitrate. Similarly darkness, red, yellow or green light favor vegetative

growth, while daylight or blue light are favorable to stromatal formation (Freeman, 1910; Bronsart, 1919).

The growing tip of the stromata remains white for a long time and is covered with a strikingly regular hymenium of palisade-like conidiophores which, if unicellular, cut off ovoid conidia; if they are multicellular, however, at any position they cut off fusiform conidia at their tips. In cultures similar conidia are cut off directly on the mycelium. In two American species, *X. tentaculata* and *X. trachelina*, the conidia do not arise directly on the stroma itself but on special branches which grow like coremia from the tips of the stromatal branches and fall off after shedding their spores.

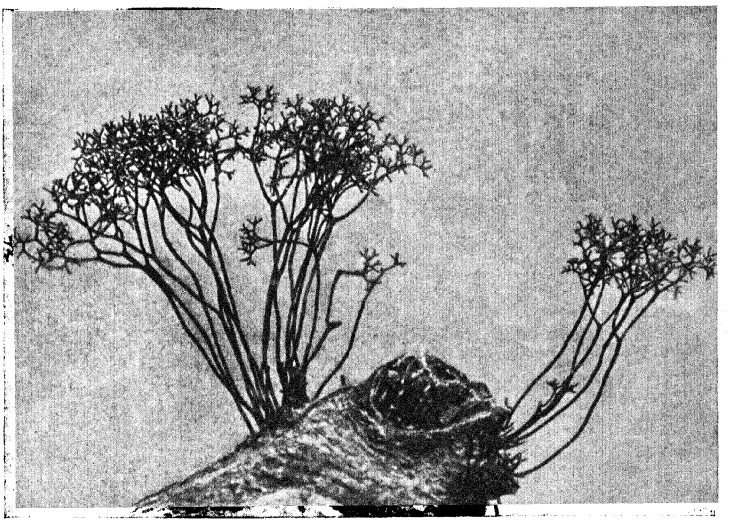


FIG. 189.—*Thamnomyces Chamissonis.* (× ⅔, *after Möller*, 1901.)

Long after the coremia have disappeared, as in the spring when *X. Hypoxylon* (Fig. 188) has borne conidia in the previous fall, the stromatal branches swell clavately in the upper part and proceed to form perithecia. As far as is known, *e.g.*, in *X. tentaculata* and *X. trachelina* (as in *Hypoxylon coccineum;* Lupo, 1922), this precedes the formation of an ascogonium without trichogyne, whose cells are first uni- or binucleate, later multinucleate (Brown, 1913).

Thamnomyces Chamissonis (Fig. 189), on hard, dry woods lying on the forest floor, forms numerous caespitose, black, erect stipes of 1 to 2 mm. diameter which grow to 7 cm. without branching. Then they branch five or six times dichotomously, the members becoming thinner and shorter with every subsequent division. The level of each division is nearly perpendicular to the previous; thus arise rigid trees up to 11 cm.

high. Each of the ultimate branches is slightly swollen and contains a single perithecium with a firm, carbonaceous wall (Moeller, 1901).

The last genus of the *Xylaria* group, *Poronia* (Fig. 190), differs from *Xylaria* and *Thamnomyces* by the discoid expansion of its fertile part. Its best known species, *Poronia punctata*, is found in the northern hemisphere on old horse dung, from which often only its fertile disc protrudes. In youth it is covered with light gray conidia. Later, at different times, helical ascogonia which end in a trichogyne, as in *Polystigma*, are formed in spots and develop in an unknown manner (Dawson, 1900).

Summary.—Here we have finished our forced march through the steppe of the Sphaeriales. In this order, especially in their parasitic representatives, pleomorphism (richness of various imperfect forms) reaches its highest point. The perfect forms are developed during the winter in our climate, where they are hastened to maturity by alternate

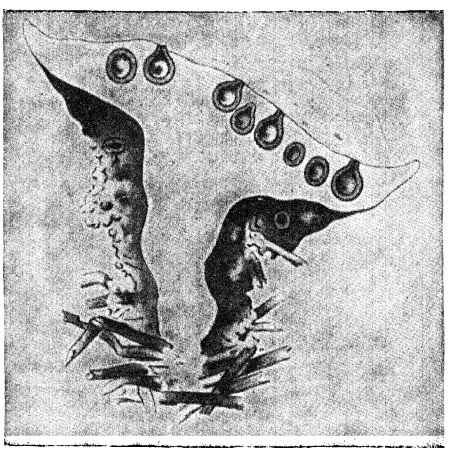


FIG. 190.—*Poronia punctata*. Longitudinal section of a stroma. (*After Tulasne.*)

wetting and drying, and hindered by the cold of winter until spring begins. Their sexual organs incline toward the Plectascales type, as do the Hypocreales, and, as the latter, still possess active antheridia. Besides they show, *e.g.*, in *Sordaria macrospora* type, wholly new peculiar forms whose significance is at present unknown. The form of fructifications vary as in the Hypocreales and, like them, attain to aggregate fructifications which begin with simpler Nectrioid cushions and ascend to highly individualized, possibly perennial stromata like *Cordyceps*. Many Sphaeriales live in consort with algae and form the Pyrenomycetous lichens, whose fungus components are still of uncertain relationship.

CHAPTER XVIII

DOTHIDEALES

It is still more impossible to give a discussion of natural groups corresponding in any way to natural relationships in the Dothideales than it was in the Sphaeriales. Originally the classification was based upon the fact that the ascigerous locules arose without perithecial wall directly inside darker, harder stromata. Thus they were regarded in part as Xylariaceae without perithecial walls. When it was subsequently recognized that in the highest Scolecosporeae of the Hypocreales, forms without perithecial walls gradually arose from forms with solitary perithecia lacking stromata, it was necessary to reorganize the Dothideales. As a matter of fact, in the last decade numerous genera and several families have been removed to the Myriangiales, not to the Sphaeriales or even to the Hypocreales; thus the Dothioraceae are mainly composed of genera removed from the Dothideales.

Even at present this process is incomplete and the classification is only provisional. At present one can best describe them as Myriangiales with polyascous loculi, thus expressing the Pseudosphaeriaceous character of the majority of their forms as, in the higher Myriangiales, the stroma consists of parallel compact hyphae rising vertically from the host. In the centrally attached forms they first spread out flabelliformly until they have attained the entire basal area of the fructification, and only then rise. In this compact mass, the loculi are formed by resorption. Since there is no perithecial wall, there is no ostiole; the top of a loculus is always formed by part of the stroma which may or may not be thickened and may or may not have a crumbling papilla, rounded bluntly or drawn out into a neck.

The main families of the Dothideales, the Dothideaceae and Phyllachoraceae, differ in the topographic position of the mature stromata; in the former, these lie on the surface but in the latter they are at first covered by host tissue.

Dothideaceae.—This family falls into three tribes: the Dothideae, the Leveillelleae and the Coccoideae. The Dothideae are the central group. Their ascus stromata arise subepidermally and are freed by the rupture of the epidermis. In *Systremma Ulmi* (*Dothidella Ulmi*), parasitic on elm leaves (Killian, 1920), the ascospores infect the young leaves during the spring rains and grow there between epidermis and cuticle to a flat, plectenchymatic crust whose elongate, palisade-like, terminal

cells cut off unicellular, uninucleate conidia. As the hyphae only penetrate the deeper leaf tissues late, the injury to the leaf is slight and the disease is only recognized in late summer (the end of August) by discolored spots. After the end of conidial production this subcuticular conidial stroma is carried away; only the hyphae in the interior of the leaf remain and intertwine between epidermis and palisade tissues to a dense plectenchyma. The cells, which in the central and basal layers are uninucleate and especially poor in protoplasm, thicken their walls

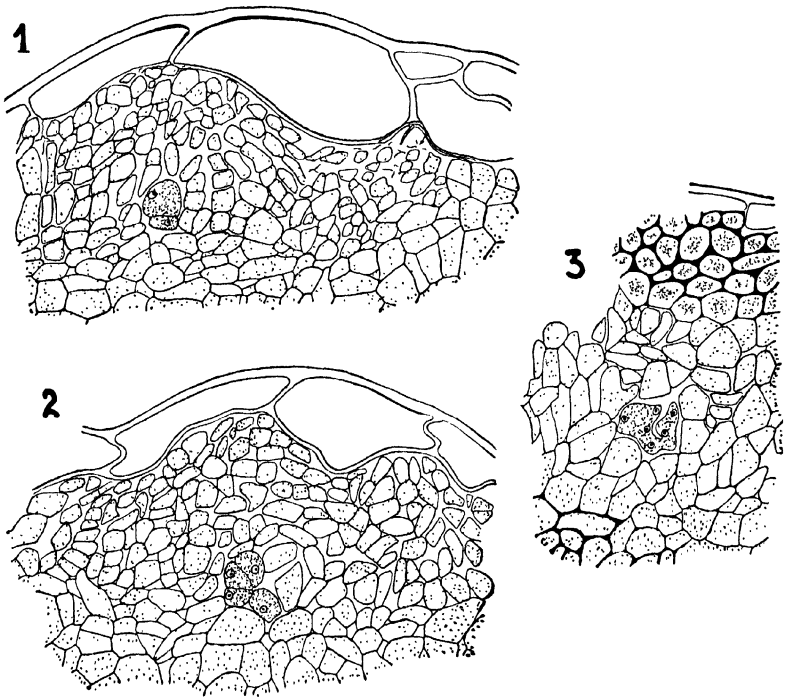


FIG. 191.—*Systremma Ulmi*. 1, 2. Sexual cells. 3. Plasmogamy. (*After Killian*, 1920.)

and turn brown. At the top of the plectenchyma the cells are richer in protoplasm; here they divide rapidly, especially in the spaces between the epidermal cells, so that the walls are usually periclinal to the mass, forming over the plectenchyma numerous small tissue swellings consisting of rows of cells, regularly septate when young.

In the middle of each of these new pads there appears a darkly staining cell which elongates and abjoints into three to four daughter cells (Fig. 191, 1 and 2). These gradually become 2 to 3 nucleate. Two of the cells develop more strongly and push the others together. Subsequently they come into open communication (Fig. 191, 3), the nuclei

migrate from one cell to the other, unite there in pairs and enter the ascogenous hyphae.

Meanwhile the cells of the top of this young meristem have flattened; they gradually thicken their walls, as happened earlier in the basal plectenchyma, and change into a cover layer.

An interpretation of this life cycle is at present impossible, as *Systremma Ulmi* is the only ontogenetically investigated species. It may be mentioned, however, that similar relations have been found in *Epichloe Bambusae* (Gäumann, 1927). One must regard the ephemeral cell series as the remains of a solitary ascogonium in which, as in *Polystigma*, parthenogamy occurs between two sexually activated cells.

From the point of view of the morphology of fructifications, the differentiation of the stroma into a conidial ectostroma and ascigerous entostroma is characteristic for *Systremma Ulmi;* and furthermore the

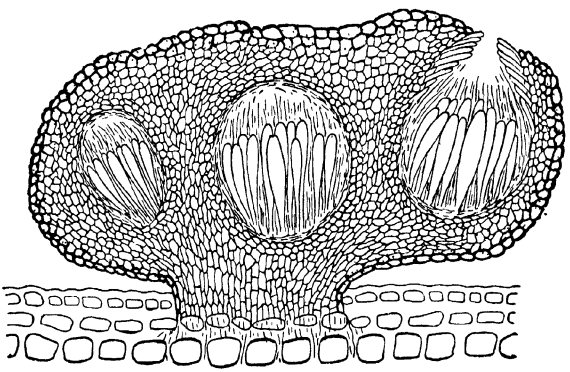


FIG. 192.—*Dothidella Derridis.* Section of stroma. (*After Theissen*, 1914.)

entostroma is first laid down as a hypodermal sterile basal stroma which only later develops fertile pads at the top. This budding of the entostroma is undoubtedly the same process as that which in the Myriangiales has led to the budding of the loculi.

If one imagines that the fertile hyphae budding from the entostroma no longer unite into pads under the epidermis but emerge from the stomata singly or fasciculately and there intertwine to form a fertile tissue, one has the second tribe, the Leveillelleae. These possess an extensive sterile subepidermal basal stroma, which is connected by numerous hyphae or mycelial strands with the fertile extramatrical ascus stroma. In systematic literature the subepidermal basal stroma is usually called the hypostroma.

This removal of the fertile ascus stroma from the interior of the leaf to the surface may be regarded as an expression of the asterinoid direction of development which we have observed in many Perisporiales,

Hypocreales and Sphaeriales and which tends to pass from endoparasitism to ectoparasitism and to the asterinoid habit, *i.e.*, to become free from the host and transfer the fructifications from the interior of the leaf to its surface. Thus we will observe how in many Leveillelleae the intramatrical hypostroma gradually degenerates; its cross section diminishes in proportion to that of the ascus stroma and the hypostroma finally shrinks to a spatially limited foot from which the fertile hyphae rise in a single column (Fig. 192). The forms which belong to this new type are united in the subfamily Coccoideae. Under these conditions, a natural line between the Leveillelleae and Coccoideae cannot be drawn, but this line rests upon a more or less arbitrary relationship of breadth between fertile ectostroma and sterile entostroma. No representative of either of these tribes has been fully investigated.

Phyllachoraceae.—While the ascus stromata of the Dothideaceae are independent of the place of their formation, and at maturity are always free, in this family they are always covered by the host tissues; in the tribe Trabutieae they lie between cuticle and epidermis, in the Scirrhieae between epidermis and palisade layer, and in the Phylachoreae in the mesophyll. The artificiality of this division is shown by the fact that the ascocarp of *Phyllachora graminis* (Phyllachoreae) is formed directly under the epidermis and later penetrates deeper.

Morphologically the Phyllachoraceae may be derived from Dothidiaceae which, on account of their exclusively intramatrical life, have undergone all sorts of modifications. Thus instead of the tuberous or pulvinate stromata of the true Dothideae, there appears a more flattened stroma. Further in most genera the cuticle or epidermis is penetrated in all directions by stromatal hyphae bound inseparably with the stroma and incorporated with it. The cuticle in the Trabutieae, or the epidermis in the remaining genera, thereby becomes an organic component of the stromatal cover layer. This is called the **clypeus.** Beginnings of such clypeal formation are already present in the Pseudosphaeriaceae (in the *Didymella Rehmii* group), in the Sphaeriales, in the Mycosphaerellaceae and in the Clypeosphaeriaceae, not otherwise discussed in this book. However, they never attain the typical structures of the Phyllachoraceae and can hardly be confused with these as the stroma forming them in the Sphaeriales contains true perithecia.

How the limits of the Phyllachoraceae, as contrasted with the Dothideaceae and simpler Sphaeriales, may best be drawn will appear only with extensive ontogenetic investigation. As characteristic of the position, a single example will be cited: the common *Phyllachora graminis*, which causes elongate black wales on grasses, has no stroma (in spite of the specific character of the order), but true solitary perithecia which are, however, held together by a common clypeus. Futhermore, it possesses true paraphyses which grow into the cavity of the perithecia (C. R.

Orton, 1924). If one wishes to regard it as derived, one must consider it as transitional to the Montagnellaceae. If one regards it as primitive it must be connected to the Mycosphaerellaceae. Which of these two concepts is more justified, is still uncertain.

Montagnellaceae.—As an appendix, a third family is considered (Theissen and Sydow, 1915) whose content and limits subsequent discussion must settle. Some of their representatives remind one of the simpler Phyllachoraceae without stromata and clypeus; others (as the higher species of *Botryosphaeria*) possess a well-developed stroma which encloses single asci (in contrast to the several asci of *Botryosphaeria*) in columnar outgrowths. The latter forms, as the *Rosenscheldia* group, are probably derived from the Dothideae or Pseudosphaeriaceae; the former, as the true Montagnelleae, probably by the loss of the clypeus from the Phyllachoraceae. As the majority of their forms are tropical, probably an ontogenetic study will not be made for a long time.

CHAPTER XIX

HYSTERIALES

With the Hysteriales begins the group of hemiangiocarpous Ascomycetes; they are Pyrenomycetes with elongate perithecia, closed during development, opening at maturity by a long slit which follows an earlier dehiscence line and almost completely uncovering the hymenium (Fig. 193, *y*). This special form of perithecium is called a **hysterothecium.** They appear depressed or conchoidal and have a carbonaceous or membranaceous wall; often they are irregularly bent. The longitudinal slit (a typical ostiole is lacking in the true forms) penetrates the upper surface as a deep groove. In damp weather, after complete maturity, the walls open like lips, more or less closing in dry weather. This process may be repeated many times. On the base of the perithecium, the asci form a broad, light-colored hymenium with paraphyses.

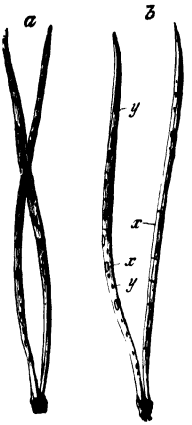


FIG. 193.—*Lophodermium pinastri*, on pine needles. *a*, one-year-old spots; *b*, two-year-old dead needles with mature, *x*, and empty, *y*, hysterothecia. (*After Hartig.*)

The Hysteriales have the elongate opening in common with the Lophiostomataceae of the Sphaeriales. According to the idea of Hoehnel (1918), these two families should be united in a new order, the Hysterostomeae; but such a rearrangement should be deferred until more ontogenetic and morphological information is secured. At any rate, the present limits of the Hysteriales include entirely heterogeneous forms, which in the future will be removed to neighboring orders. According to Lindau (1897), they may be divided into five families: the Hypodermataceae, whose hysterothecia are embedded in the substrate, overgrown by a layer of host tissue with which they form a clypeus; the Dichaenaceae, hysterothecia membranous—leathery; Ostropaceae, hysterothecia thick, almost corky, at first embedded, later erumpent and free; Hysteriaceae, hysterothecia carbonaceous, black; and Acrospermaceae, hysterothecia horny, brown, free at the top, but with the bottom somewhat embedded in a subiculum.

Only a few Hypodermataceae are of economic significance, especially *Hypodermella* (ascospores unicellular, lachrymiform) *Hypoderma* (ascospores two-celled) and *Lophodermium* (ascospores unicellular, elongate) which cause a premature drying and abscission of coniferous needles: *L.*

pinastri, *Hypodermella sulcigena* and *Hypoderma deformans* on pines, *L. macrosporum* on spruce, *L. nervisequum* on white fir, *Hypodermella laricis* and *L. laricinum* on larches, etc. (Tubeuf, 1901; Haack, 1911). The needles of the young plants are infected in the summer by the ascospores, and begin to turn yellow, browning in zones. In the first year, the fungus forms pycnia, in the second and third, when the needles have fallen, hysterothecia.

In *Lophodermium hysterioides* on *Crataegus Oxyacantha*, the mycelium from the germinating spore penetrates the stoma and forms a small sclerotium in the substomatal cavity. This then gradually invades the mesophyll. The pycnia develop under the cuticle and form flat discs of the *Leptostroma* type. Likhité was unable to effect germination of conidia. About the end of January the apothecia develop, often in the vicinity of the pycnia. In the hysterothecial stroma large multinucleate cells give rise to uni- or binucleate spiral ascogonia, lying in the plane of the hysterothecium. Pores form in the cell walls and nuclear migration is probable, although not observed. Paraphyses develop from spherical mother cells with many small nuclei. In April and May ascogenous hyphae arise from some of the ascogonial cells, while the rest degenerate and develop, without the formation of hooks (Killian and Likhité, 1924; Likhité, 1926).

Close relatives of the Hysteriaceae form with species of *Trentepohlia*, crustose lichens, which are common on tree trunks, especially in the tropics, *e.g.*, *Graphis scripta*.

CHAPTER XX

HEMISPHAERIALES

With the Hemisphaeriales, we have left the classic Pyrenomycetes and passed to the Discomycetes. As their name signifies, the Hemisphaeriales form a group of families which originally were included in the Sphaeriales (including Perisporiales and Hysteriales), but have been removed to a new order on account of their disciform, pseudosphaerial fructification whose scutellate cap, with a peculiar, generally radial structure but lacking an ostiole, ruptures irregularly. They are intermediate between the Pyrenomycetes and the Phacidiales. The Hemisphaeriales are a temporary, artificial order, containing a series of generally parasitic families.

Stigmateaceae.—This family is distinguished by the subcuticular position of the fructification, as in the Trabutieae. *Stigmatea Robertiani* (*Hormotheca Robertiani*) on *Geranium Robertianum* (Theissen, 1916; Theissen and Sydow, 1917; Klebahn, 1918; Killian, 1922) appears on the leaves of the host, in damp weather in summer and fall, in the form of small spots up to 3 mm. across. It continues to develop through the winter. The mycelium lives only on the outer surface of the infected leaves, generally on the upper surface, occasionally on the lower surface, often on both. Between epidermis and cuticle, it forms a continuous membranous layer which neither penetrates the deeper tissues by hyphae nor the epidermal cells by haustoria (Fig. 194, 1). In the central part, it gradually thickens into a flat plectenchymatous cushion in whose interior there appear two deeply staining uninucleate cells, in one or several neighboring positions, without conidial production (Fig. 194, 2). Generally only one develops while the other is resorbed. This one cell goes through several nuclear divisions, elongates and develops, by the formation of several septa, into a slightly bent, fertile hypha (Fig. 194, 3). Its innermost cell, *i.e.*, that which lies next the middle of the plectenchyma, elongates again perpendicular to the leaf surface and develops to a binucleate ascogonium with a peculiar receptive process at its tip (Fig. 195, 1). Another cell of the fertile hypha develops to a binucleate antheridium. The two organs come in open communication with each other, the male nucleus migrates to the ascogonium (Fig. 195, 2), after repeated division unites with the female nucleus and migrates into the ascogenous hyphae which later proceeds to the formation of asci between true paraphyses.

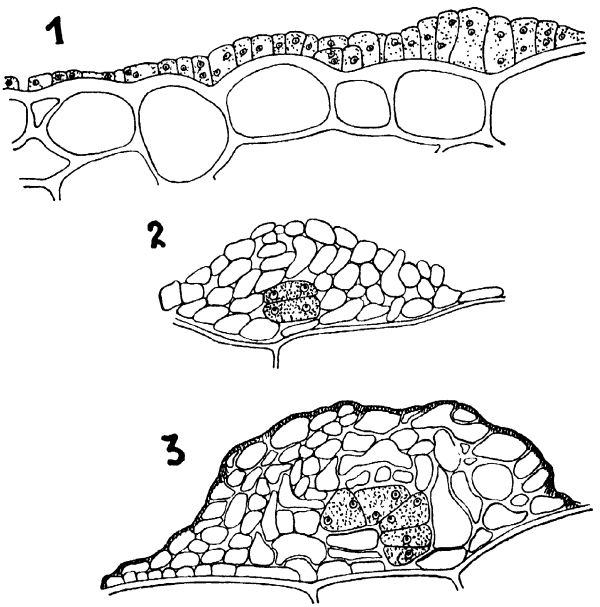


FIG. 194.—*Stigmatea Robertiani.* Development of fructification. 1. Section through a sterile plectenchyma on the upper surface of a leaf. 2. Young fructification fundament. 3. Young fructification with a fertile hyphae. (× 1,000; *after Killian*, 1922.)

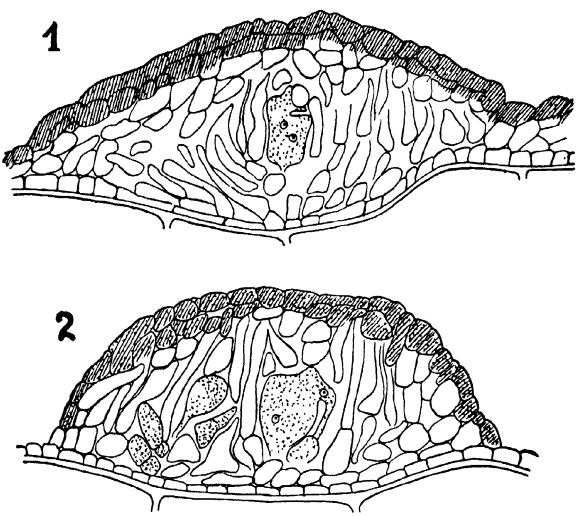


FIG. 195.—*Stigmatea Robertiani.* 1. Young fructification with a mature ascogonium. 2. Plasmogamy. (× 1,000; *after Killian*, 1922.)

Meanwhile the surface of the plectenchymatic cushion has become brown and chitinized. At its tip is differentiated a small papilla which later breaks off and leaves a circular hole through which the ascospores escape (Fig. 196). At the periphery, the aliform surface layer extends over the edge of the narrow perithecium and ends blindly. Thus it

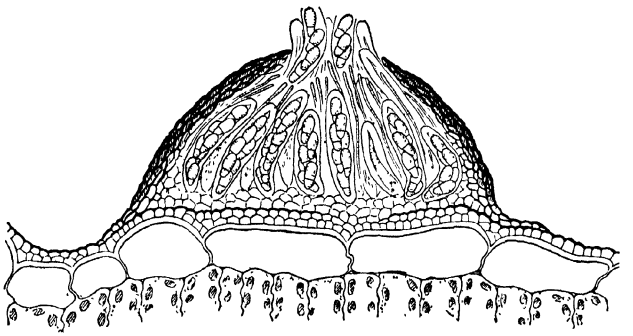


FIG. 196.—*Stigmatea Robertiani*. Section through a fructification. (× 341; *after Klebahn*, 1918.)

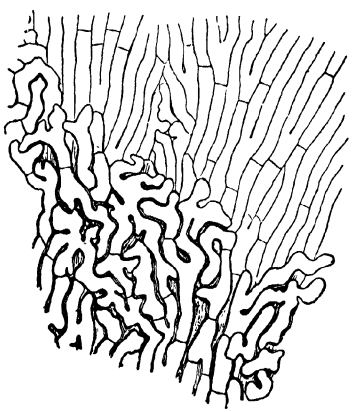


FIG. 197.

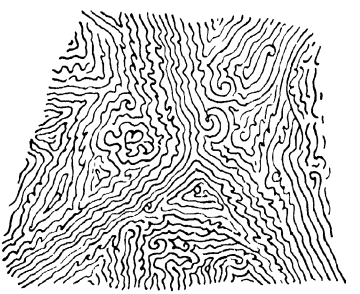


FIG. 198.

FIG. 197.—*Stigmatea Robertiani*. Surface view of the subcuticular mycelium which merges at its lower edge with the outer layer of the fructification. (× 804; *after Klebahn*, 1918.)

FIG. 198.—*Stigmatea Robertiani*. Portion of the edge of the fructification. (*After Theissen and Sydow*, 1917.)

forms only the central part of a scutellate cover which gradually continues outward into the original mycelial membrane (Fig. 197). Seen from above, the elements radiate in waves and themselves often form secondary centers of radiation (Fig. 198).

This life cycle of *S. Robertiani* is notable in three respects. First, its fructification no longer has a perithecial wall, but is an apothecia-like

cushion which has only a covering and no specially differentiated basal layer. Seen from above, its development appears as if a round or elliptical portion of the thallus arches up and begins to thicken, while an ascigerous hymenium forms under the arch. This process is called pycnosis in systematic literature, and the fructifications thus formed **pycnothecia.** In the second place, the formation of ascogenous hyphae is preceded by a true sexual act, which on the whole takes place in organs of a structure like that of *Claviceps purpurea* of the Hypocreales. In the third place, under the same cover layer, several ascogonia may be active, so that under certain conditions the ascogenous hyphae radiate from several centers. This last peculiarity suggests a tribe of the Stigmateaceae, the Munkielleae, ontogenetically still unknown, which, with a structure otherwise the same, has under the same cover several hollow, arched discs of asci.

Polystomellaceae.—This family is characterized by its ascomata arising only on the surface while the mycelium is parasitic in the interior of the leaf. They show a great similarity to the Coccoideae and Leveillelleae of the Dothideaceae. They may be briefly described as Coccoideae or Leveillelleae with radial cover layers. As in the Coccoideae, so also in certain Polystomellaceae, the fructifications are rooted in the host tissue by a central column; in other Polystomatellaceae, as in the Leveillelleae, several of these columns may be present.

According to the outline of the loculi, the family may be divided into two tribes, the Polystomelleae with round, and the Parmulineae with linear loculi. This distinction, however, is only of value for mature perithecia; thus in many species of *Hysterostomella* the young loculi at the edge of the turf are round, developing their linear outline only at maturity. In this linear outline of the Parmulineae, people have tried to see a relation to the linear opening of the Hysteriales, and hence have called the Parmulineae Hemihysteriaceae. It seems here to be a question of convergence phenomena, however, for from the irregularly tearing slit of the Parmulineae to the labiate opening of the typical Hysteriales, the step is just as great as from the opening of the Dothideales to the ostiole of the typical Sphaeriales. In any case the originally circular perithecium shows a further development.

Hysterostomella discoidea (*Parmularia discoidea, Schneepia discoidea*) corresponds to the Leveillelleae type of the Dothideales. In West Java, it is parasitic on fronds of *Polypodium longissimum* and there forms more or less circular stromata up to 3 mm. in diameter. The infected leaf surface is slightly vesicular and the stroma arches over convexly. In the hypostomatal cavities, the hyphae collect in brown or violet tangles, and then push outward to the leaf surface in perpendicular prosenchymatic columns (Fig. 199). Here they expand horizontally. Generally the hyphal bundles are only present in the central portions of the stroma

while the outside of the flat stroma has no direct connection with the substrate. In contrast to the Stigmateaceae, the basal layer of the stroma is dark, and hence definitely recognizable as such. Again, differing from *Stigmatea Robertiani* and like the Munkielleae, the numerous radial

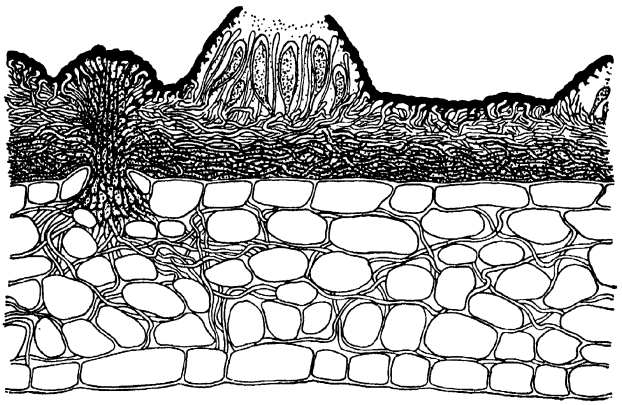


FIG. 199.—***Hysterostomella discoidea.*** Section of ascus stroma on lower surface of leaf. (× 250; *after Arnaud*, 1918.)

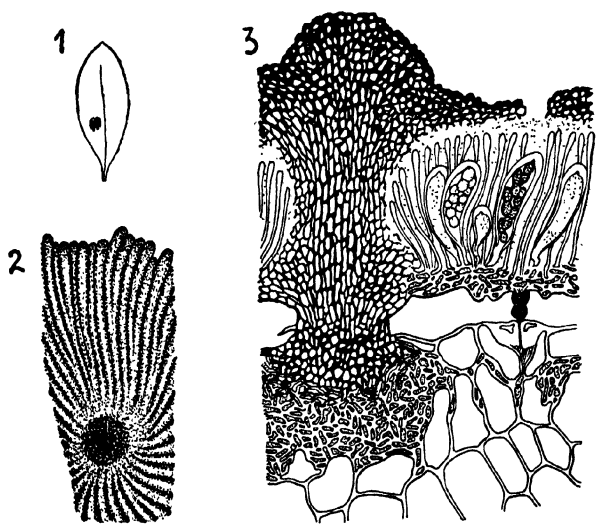


FIG. 200.—*Cycloschizon Alyxiae.* 1. Lower surface of *Alyxia* leaf with ascus stroma. 2. Part of surface of young ascus stroma. (1 × ⅔; 2, 3 × 250; *after Arnaud*, 1918.)

loculi, generally under the same covering layer, are irregularly sinuous, recurved and often forked acutely.

Cycloschizon Alyxiae (*Maurodothis Alyxiae, Dielsiella Alyxiae*) in Australia and Tasmania is parasitic on the leaves of *Alyxia buxifolia.*

The mycelium penetrates for short stretches, and hyphal columns emerge on the lower sides of the leaves in numerous places where each develops to a small flat fructification. Thus these small fructifications are close together and often form groups up to 7 mm. cross section (Fig. 200, 1). At times they are so close that they look like a single crust; the oldest lie in the center, the youngest at the periphery. At maturity, the single fructifications are circular, 0.5 mm. in diameter and divided in the middle by a hemispherical knob with radial furrows (Fig. 200, 2). In contrast to *Hysterostomella*, only one central column is present in each fructification (Fig. 200, 3), while in *Hysterostomella* as many as half a dozen are to be

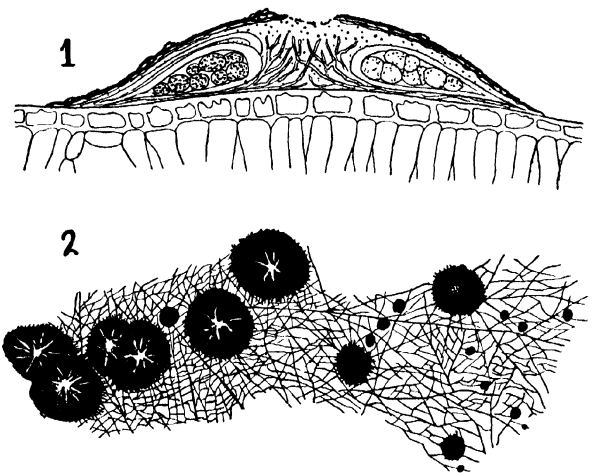


FIG. 201.—*Asterinella Puiggarii*. 1. Section of recently opened fructification. 2. Part of mycelium, showing young and mature fructifications. (1 × 250; 2 × 34; *after Arnaud*, 1918.)

seen. As a substitute for this, the stromata of *Cycloschizon* put out from time to time peculiar sinkers which penetrate the interior of the leaf through stomata, serving to anchor and to nourish the stromata (Fig. 200, 3 right). In contrast to *Hysterostomella*, only one loculus, instead of several, is present in the fructification. While in Fig. 199 one must imagine, to right and left, cross and longitudinal loculi, for *Cycloschizon* all portions of the loculus are visible in Fig. 200, 3. These belong to a single loculus which circumscribes the hyphal knob under the radially striate cover, like a horseshoe or a ring. Hence at maturity the cover does not rupture radially, as in *Hysterostomella*, but perpendicular to the furrows of the cover with the sterile knob as the center; only subsequently may this circular split fray out by short radial slits.

Microthyriaceae.—This family shows the purest type of asterinoid habit. It has given rise to the idea of asterinoid life forms (Theissen,

1912, 1914; Theissen and Sydow, 1917; Hoehnel, 1917, 1918; Arnaud, 1918; Doidge, 1920).

It is difficult to describe briefly the characters of the Microthyriaceae, as all their forms merge into each other and into related families. In any case, they are usually superficial ectoparasites. The ascus stromata are provided with radial covers. In the Microthyrieae there is no aerial mycelium at maturity; in the Asterineae, the mycelium is persistent, dark colored, squarrose, asterinoid, often like the sooty moulds, aerial (Figs. 201 and 202). As in the Perisporiaceae, so also in the Asterineae, there



FIG. 202.—*Lembosia Bromeliacearum*. 1. Section of fructification (× 250). 2. Central portion of mycelium bearing a fructification (× 34; *after Arnaud*, 1918.)

are formed on the hyphae numerous specialized branches, hyphopodia and stigmopodia. As there, so also here the stigmocysts may develop to fructifications. Besides, the formation of fructifications may take place directly under any hypha so that the hypha lightly touches the young perithecium or it may—in the species without mycelia—take place directly on the transitory germ mycelium which develops from the ascospores.

In all these cases, the mother cells first divided to small cell complexes which either remained discoid, flat and one layered or grew into knob-like papillae, which frequently persisted a long time (Fig. 203, 1). This layer grows centrifugally, so that the newly added cells have an elongate prismatic outline. Thus there is formed under the main hypha close to the

leaf, a thin, light-brown fruit disc, of radiating prosenchyma, in one layer at the periphery, with pseudoparenchyma in the middle. While this develops to its definite limits, as in *Stigmatea*, it begins to rise from the center outward, being pulled from the developing core, and to arch up like a flat spherical cap or hemisphere. Thus the generative hyphae are torn off, with increasing tension the cover is soon ruptured, forming an opening which may be widened by histolysis. The asci arise singly in the loculi and are generally eight spored.

The development of the fructifications of the Microthyriaceae, often called thyriothecia has puzzled the systematist for a long time. As

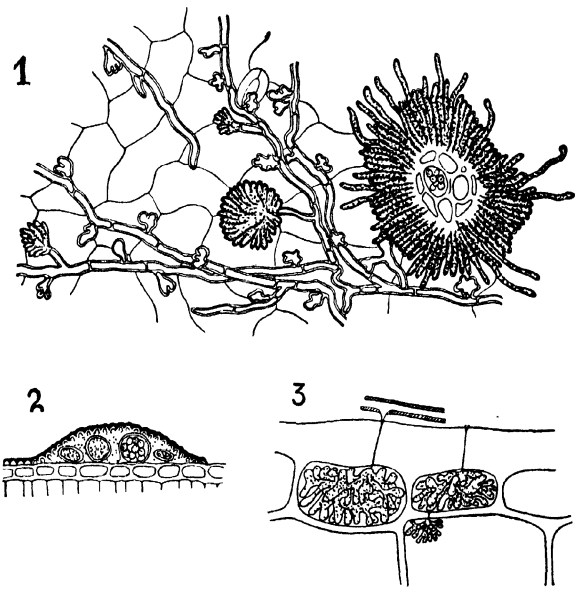


FIG. 203.—*Dimerosporium Veronicae*. 1. Group of fructifications on lower side of a leaf. The older has ruptured at the top. 2. Section of fructifications. *Asterina Usterii*. 3. Hyphae and epidermal haustoria on lower surface of a leaf. (1 × 7, 2 × 250; 3 × 620; *after Arnaud*, 1918, *and Maire*, 1908.)

the **thyriothecia** are not oriented by the mycelium but by the host, their generative hyphae hang downward. Hence they are inverted, *i.e.*, their morphological base is at the top. Since the Microthyriaceae have been considered connected, through a series of intermediate forms, with *Meliola* of the Perisporiaceae, the thyriothecia must be regarded as halved perithecia, *i.e.*, as perithecia in which the tip (lying beneath) has not developed further for lack of space. According to this conception, since the radial cover layer remained unexplained, the thyriothecia were considered complex structures, *i.e.*, as upright perithecia, lying free from the substrate, protected by their radial shield and no longer needing a

special perithecial wall, gradually reduced to a naked core. It seems better to interpret the thyriothecia in the light of the pycnothecia and the ascomata of *Plectodiscella* and to defer further conclusions until ontogenetic

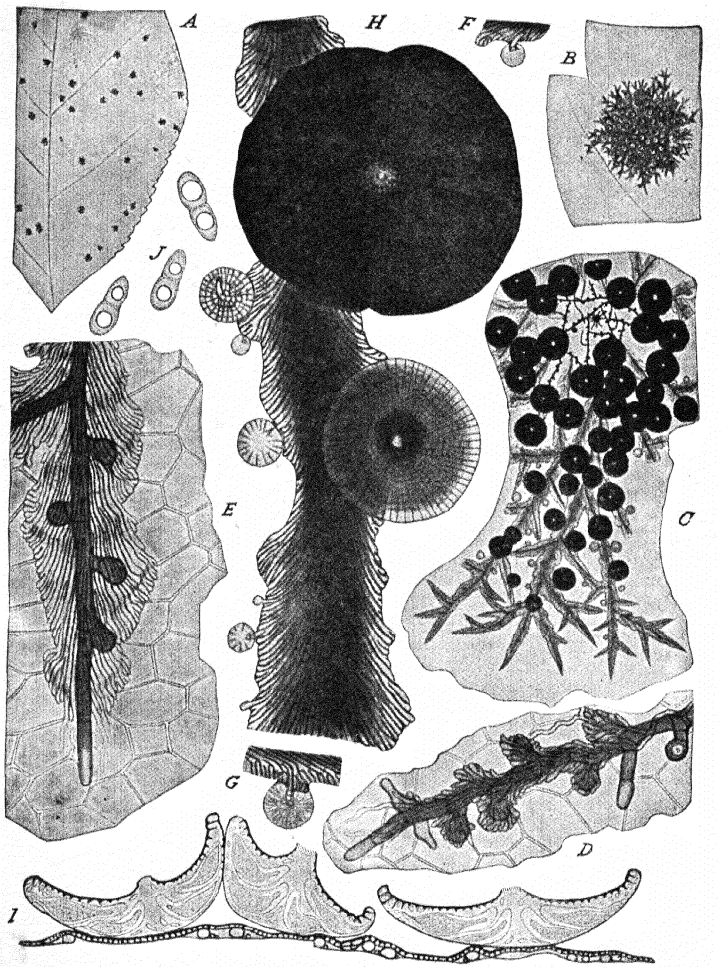


FIG. 204.—*Trichothyrium fimbriatum* on *Meliola*. *A*. Upper surface of leaf showing points of infection. *B*. The same enlarged. *C*. Periphery of mat. Some mycelium of *Meliola* still visible in the middle. *D*, *E*. Hyphal bands. *F*, *H*. Formation of fructifications. *I*. Section of immature fructifications. *J*. Ascospores. (*A* × ¾; *B* × 8; *D* to *I* × 285; *J* × 750; *after Arnaud*, 1918.)

investigations of the Microthyriaceae are made. The actual striking correspondence between the habit of *Meliola* and of the Microthyriaceae would then be regarded as convergence phenomena.

The Microthyriaceae include about 40 genera with about 400 species, chiefly of the tropics and subtropics. Just as in the Polystomelleae–Parmulineae series, a gradual transition occurs from round (Fig. 201) to linear (Fig. 202) fructifications, since in *Hysterostomella* even the linear fructifications in youth have a rounded outline. At present no species of economic importance is known.

Trichothyriaceae.—The representatives of this family (Theissen, 1912; Hoehnel, 1917; Arnaud, 1918) may be regarded as Microthyriaceae which have become specialized for parasitism on other, especially asterinoid, fungi. The originally independent hyphae cling together in brown bands (Fig. 204, *D* and *E*) which cover the mycelium of the host and occasionally are confused with it. As the members of this family do not themselves directly parasitize leaves, their fructifications lie on their own mycelium unprotected beneath by the cuticle of the host. Consequently the basal stromatal parts attain a more marked cover layer character: they become brown and pseudoparenchymatic (Fig. 204, *I*). In some genera, as *Loranthomyces*, parasitic on the stromatic Sphaeriales, the fructifications appear entirely inverted and the asci hang down from the morphological base above. These inverted thyriothecia are called **catothecia** by Hoehnel (1917). Unfortunately their ontogeny is entirely unknown.

CHAPTER XXI

PHACIDIALES

The Phacidiales are connected on one side to the Hysteriales, on the other side to the Dermateaceae and Bulgariaceae, in the Pezizales. In time they will probably be divided between these two groups. They are Discomycetes with ingrown or superficial perithecia, surrounded or only developed above, rupturing at maturity by several irregular slits above. According to one's definition and personal viewpoint, they may be divided in different ways. Lindau (1897) divides them into three families: the Stictidaceae, with slightly fleshy, bright-colored perithecia and Tryblidiaceae and Phacideaceae with black leathery or carbonaceous, perithecia, which in the former possess a thick hypothecium and project above the substrate; the latter, having only a thin, poorly developed hypothecium, remain immersed in the substrate or in their stroma. Hoehnel (1917) divided the order in the narrower sense into six families based on the situation of the fructifications in the host tissue: the Schizothyriaceae with flat fructifications upon the cuticle, the Leptopeltinaceae with subcuticular fructifications, the Dermopeltinaceae with intraepidermal fructifications, the Phacidiaceae with subepidermal or still deeper fructifications, the Phacidiostromataceae whose fructifications include the whole tissue between the epidermal layers of leaves, coalesce with them or (in ramicolous forms) are sunk deep in the stem tissues and here coalesce with the stem epidermis, and the Cryptomycetaceae with fructifications under the periderm of stems and twigs.

The ontogeny of *Cryptomyces Pteridis* (Killian, 1918) and *Rhytisma acerinum* (Jones, 1925) is known. *C. Pteridis*, causing a leaf roll of the brake, belongs to the Phacidiaceae of Lindau's treatment, to the Cryptomycetaceae of Hoehnel's. At the beginning of the warm spring rains, the ascospores of the over-wintered fructification infect the young fronds of *Pteris*. At first the hyphae grow intercellularly, then intracellularly in all directions and intertwine in the hypostomatal cavities to flat cushions whose apical cells cut off fusiform, uninucleate conidia (Figs. 205 and 206). Conidial formation continues until the beginning of cold weather. A protective layer is formed, changing the cushions to flat, irregular pycnia.

During the summer the fundaments of the ascus fructification are formed as small plectenchymatic knots in the hypostomatal cavity. The cells of the plectenchyma lying between the guard cells have a

denser content and deeper staining properties. They grow to fertile hyphae, which bore under the plectenchyma in a group and reach a length of six cells (Fig. 207, *A*). Meanwhile the knot thickens the cell walls on its outer surface, and becomes a flat, brown, sclerotic mass. The fertile hyphae stow themselves on the hard basal peridial layer, bend irregularly and fork.

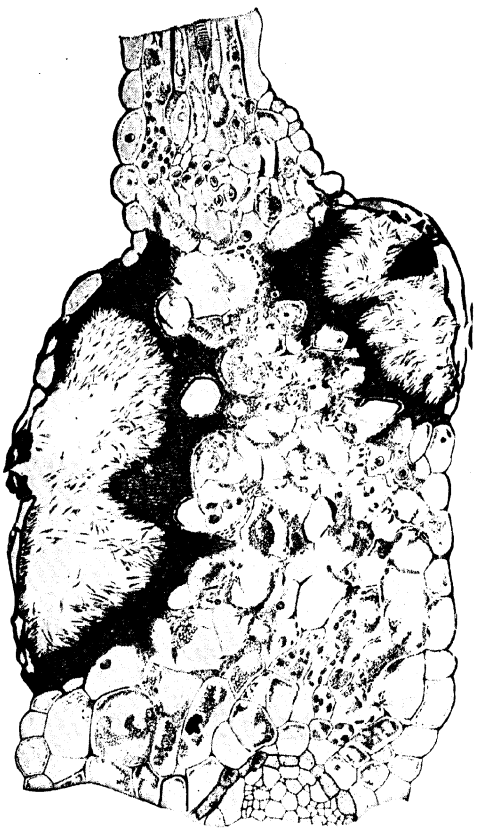


FIG. 205.—*Cryptomyces Pteridis*. Section of young hypertrophied fronds of the brake covered with acervuli. (× 330; *after Killian*, 1918.)

The further development proceeds from the three more strongly developed end cells (Fig. 207, *A*, cells *a*, *b*, *c*). Cell *a* later elongates so that only the subterminal cell *b* and the terminal cell *c* retain their characteristic cubical appearance. In late summer, the subterminal cells of two neighboring fertile hyphae develop copulation papillae toward each other and the nucleus migrates from one cell to the other while the rest of the fertile hypha collapses and disappears.

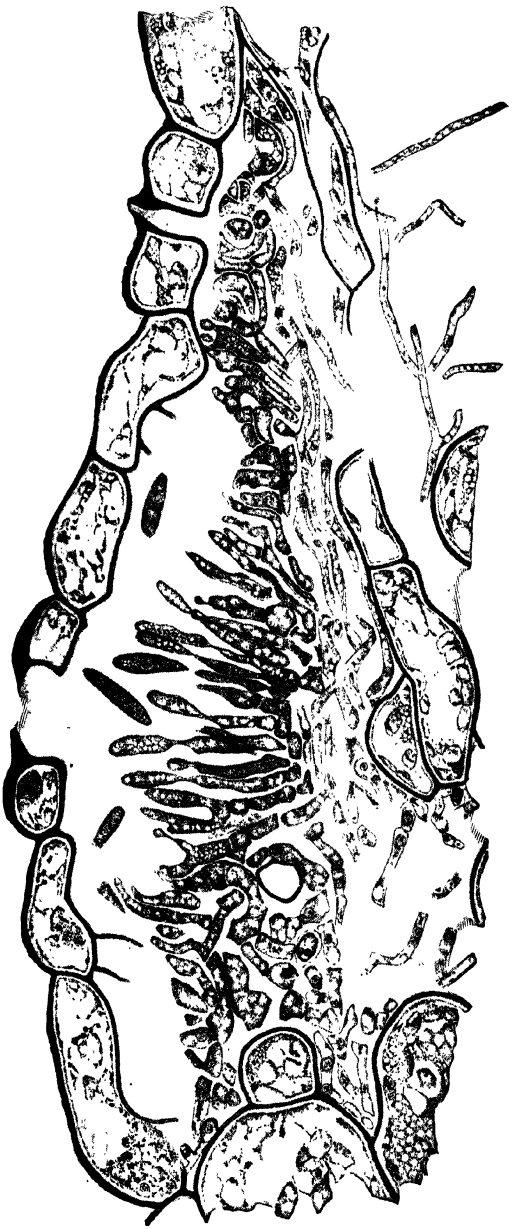


FIG. 206.—*Cryptomyces Pteridis*. Section of a young acervulus in the substomatal cavity. (× 550; *after Killian*, 1918.)

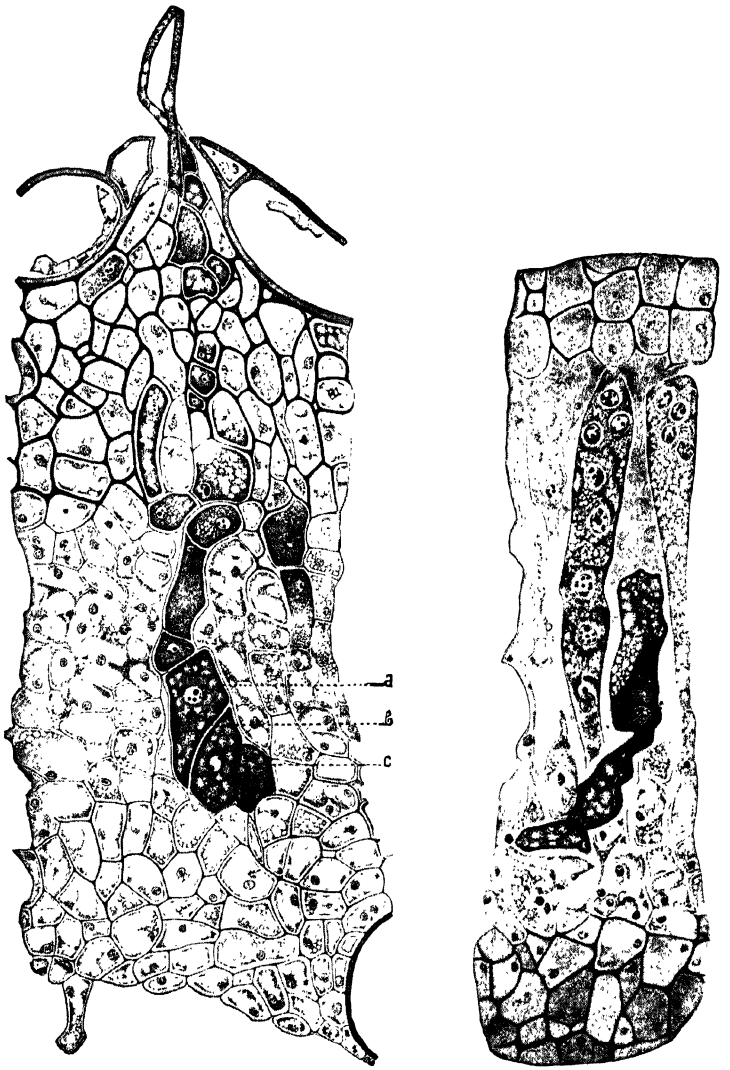


FIG. 207.—*Cryptomyces Pteridis*. *A*. Section of a young ascus fructification with immature fertile hyphae. Above, the apical layer, below, the basal (× 830). *B*. Older stage with young asci (× 550). (*After Killian*, 1918.)

As in *Venturia*, there is now a rest period which lasts through the winter. In spring, the binucleate cell develops in an unknown manner ascogenous hyphae which form 8-spored asci (Fig. 207, *B*).

This peculiar ontogeny may not be interpreted at present, since *Cryptomyces* is still too isolated morphologically. In certain relations it reminds one of *Penicillium crustaceum* as there the ascogenous hyphae, so here the fertile hyphae grow like foreign bodies in the plectenchyma of the fructification and parasitize it in a certain sense; this relation finds its explanation in the fact that at that time only the tissue of the fructification can furnish nourishment, since the leaf of the host is already exhausted. It is also suggestive of the relations of the oöblastema filaments to auxiliary cells in the red algae.

In regard to the origin of the fertile hyphae, *Cryptomyces Pteridis* is reminiscent of *Systremma Ulmi;* as in the latter, they are the apical cells of the parenchyma of the fructification which, by renewed growth, change the sclerotoid tissue body to true ascomata. Only in *S. Ulmi* this growth takes place upward from the tissue body, while in *C. Pteridis* from above down into the tissue body. It is possible that this localization of the meristem at the top of the tissue body is connected with the oxygen requirements of the fertile hyphae.

In form of fertile hyphae, *C. Pteridis* is almost unique. While in the previously discussed forms, the ascogonia, with the exception of *Sordaria macrospora* in the Sordariaceae, generally are helical, in *C. Pteridis* the fertile hyphae (antheridia and ascogonia) are elongate. To use an expression of Killian, they form a parallel thread type. It is possible that they must be regarded as end forms in a sense which will be again met in the Pezizales, in the *Leotia–Spathularia* series of the Geoglossaceae and the *Icmadophila–Baeomyces* series of the discomycetous lichens, in which the ascogonia (which alone are formed in these species, since the antheridia are suppressed) gradually lose their specific form, finally becoming vegetative hyphae filled with reserves. In this manner, the fertile hyphae of *Cryptomyces* may be regarded as an (ideal) step in the direction of the pseudogamy which takes place in the Uredinales (*e.g.*, in the aecia between two specialized hyphae).

The other forms so far studied give no answer to this question. In *Coccomyces hiemalis* (Higgins, 1914), the leaf spot of cherry, and *Phacidium repandum* on *Galium rubioides* (Satina, 1921), helical ascogonia with trichogynes of the *Polystigma* type were observed.

In *Rhytisma acerinum*, one of the Dermopeltinaceae of Hoehnel, the ascogonia are elongate and no longer typical, while there are no antheridia. The hyphae penetrate maple leaves in all directions from the spot of infection and fill the epidermal cells of the upper surface of the leaf, less often those of the lower side, with a dense tissue. The walls between the epidermal cells are broken and gradually dissolve so that the hyphal

tissue forms a long continuous plectenchymatic stroma. In the central parts of the stroma, numerous hyphal tips rise within the limited region from the plectenchyma, form a regular palisade and, after June, cut off an enormous number of uninucleate conidia. Their pressure ruptures the outer epidermal wall, pieces of which are occasionally raised by the conidial mass as upon a column, and the conidia are liberated in a milky drop. Morphologically, thus, *R. acerinum* does not form pycnia, as systematic literature often states, but acervuli like *Cryptomyces Pteridis*.

Like the conidial layer, the apothecia are formed in the epidermis of the upper surface of the leaf, chiefly on the peripheral parts of the stroma. The majority of them are formed *de novo*, but a few are laid down in the exhausted acervuli. In the fall, the whole stroma changes to a sclerotic tissue which blackens on the upper surface, less often on the under surface (*i.e.*, toward the palisade layer of the leaf). In the interior of the plectenchyma are differentiated numerous apothecial cavities filled with loose hyphal tissue and covered by a thick-walled, pitch-black epithecium (and the outer epidermal wall) and below rest on a somewhat broader, brighter hypothecium (with the inner epidermal wall).

In each apothecial fundament are formed several ascogonia which consist of a uninucleate stipe cell, 2 to 3 multinucleate ascogonial cells and a uninucleate trichogyne cell. The septa between the ascogonial cells break down, as in *Ascobolus citrinus* of the Pezizales (Fig. 227); the nuclei pair parthenogamously and migrate into the ascogenous hyphae, which coil and grow out again, as we have already seen in *Aphanoascus cinnabarinus* of the Plectascales. Eight ellipsoidal ascospores are formed and elongate to filaments. They may be shot up for 1 mm., probably as a result of contraction of the stroma in dry weather. Thus the swollen paraphyses (which are formed from the loose hyphal tissue between the epi- and hypothecium) press the asci which in turn squeeze out the spores and secure their dispersal by air currents.

While the asci are still in the uninucleate stage in early spring, a dehiscence zone about 12 cells wide is formed in the middle of the apothecium in the lower fourth of the epithecium. The cells of this zone become disorganized, causing a narrow slit which, by the degeneration of the bordering apical layers, expands somewhat at the top. In the lowest fourth of the epithecium, below the horizontal slit, lateral growth begins so that this lower fourth arches downward into the apothecial cavity. By this lateral growth the upper layer of the epithecium is ruptured. Finally the pressure of the ascospores ruptures the lower wall layer under the split, and the edges spring back, exposing the hymenium. Unfortunately these relationships cannot be figured in this book, as the work of Jones was only available to the author after the figures had been sent off for reproduction.

Rhytisma acerinum causes the tar spot of maple; the biological form *platanoides* (K. Muller, 1913) lives mainly on *A. platanoides*, less on *A. platanus* and *A. campestris;* while forms *Pseudoplatani* and *campestris* are specialized on *A. Pseudoplatanus* and *A. campestris.*

Because of the obscure character of the Phacidiales, we will mention only that several forms, as the above *Coccomyces hiemalis*, *C. lutescens* and *C. prunophorae* on cherries and plums (Higgins, 1914) and *Phacidiella discolor*, the cause of a canker of the apple in the Caucasus (Potebnia, 1912) form both macro- and microconidia in acervuli. In the latter species, the hyphae may develop sprout mycelium under certain conditions of growth.

CHAPTER XXII

PEZIZALES

In the Pezizales are grouped all fleshy Discomycetes. They are characterized by the special structure of the fructifications which, as briefly mentioned in the introduction to the Ascomycetes, are called apothecia. A diagrammatic cross-section of a lichen apothecium is given in Fig. 208.

This discoid fertile layer (the ascus hymenium or thecium) is designated as *t*. It generally lies free in the later stages of development, as

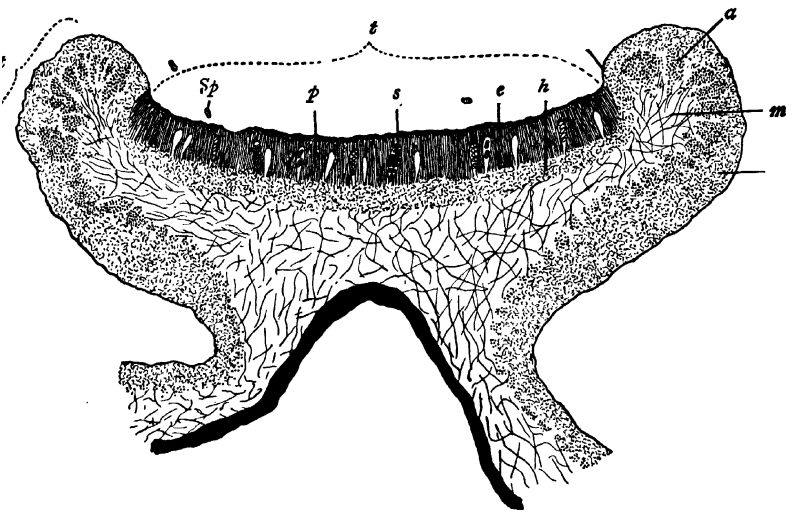


FIG. 208.—*Section* of the apothecium of *Physcia pulverulenta*. (*After Nienburg*, 1913.)

shown in Fig. 208; in the early stages it is arched over by a special cover layer which appears approximately in the direction of the dotted line in Fig. 208 and only later, with the expansion of the hymenium, is reduced to threads. Forms which, like these, begin their development angiocarpously and end gymnocarpously are called hemiangiocarpous.

Histologically, the fertile layer is composed of asci which form the ascospores *Sp* and of the paraphyses *p*. The asci belong to the diplont, but the paraphyses and the rest of the fructification to the haplont. The paraphyses show their haploid nature in teratological cases, *e.g.*, *Fabraea*

Fragariae, where they may proceed to form conidia. In certain forms they do not arise directly from the ground tissue of the fructification but from large storage cells. Their fate varies in the different families. In one they swell, as in many Sphaeriales, into a structureless gel, in another they are persistent and partly intertwine over the tops of the asci to a thin, brightly colored layer, the **epithecium** *e*; it is this cover layer which, seen from above, gives the characteristic color to the apothecia.

Besides the paraphyses in the hymenium of many forms there are peculiar paraphysoid setae, which also belong to the haplont (not shown in Fig. 208). While the true paraphyses are thin walled, hyaline and multiseptate, the setae are thick walled, brown and always unicellular. In the young stages they bend together (in the hemiangiocarpous forms, after the rupture of the layer covering the young fructification) and form a sort of sheath over the developing hymenium. Later they are pushed aside and at most surround the disc. In the purely gymnocarpous forms, whose hymenium is free and exogenous, they often remain scattered over the hymenium during its development. In this case they rise far below in the hypothecium and secrete a brown gluten at their tips. This gluten flows over the surface of the hymenium, which in this case is chiefly formed of the capitate ends of paraphyses, and there forms a structure which, at first glance, might be confused with the epithecium. In this gel there often live a large number of bacteria which assist in the rapid decay of the fructification.

Under the hymenium is the **hypothecium** *h*, which forms the paraphyses directly and the asci indirectly. In some families the layer which bears the hymenium, the hymenophore, is marked by a denser structure or darker color; in systematic literature it is called the **exciple.** In the ideal case, the hypothecium projects beyond the edge of the ascus layer and forms the rim of the saucer or bowl *pt*; when this rim is distinguished from the other tissue by a darker color, it is called a **parathecium.** In certain forms the outer wall of the hypothecium is pseudoparenchymatic and often darker in color (*r* in Fig. 208).

The previously named layers and organs are all an inheritance of the fungi; in the special case of the lichens mentioned here, they may be surrounded by a thalline margin (exciple) which forms the **amphithecium;** this is usually similar in structure to that of the thallus of the lichen in question and is generally composed of a cortex *r*, the algal layer *a* and the medulla *m*, which is connected to the hypothecium either directly or by a second algal layer.

In nature, comparatively few apothecia have simultaneously all the different layers here mentioned. In the lower forms, the apothecia are of simpler structure and consist of a stromatic cushion, with an ascigerous hymenium. In the higher forms they are much modified, so that the fructifications in their histological differentiation, formation of latex

vessels, extensive formation of special tissues, etc., remind one of the structures of pileate fungi, or of the stems and leaves of cormophytes. An attempt has been made to use the structure of the apothecium for systematic classification of the Pezizales, especially to distinguish fundamentally between gymnocarpous (exogenous) and angiocarpous (endogenous) forms and to unite the gymnocarpous forms in the series with the Helvellales and the angiocarpous forms in the Pezizales. Ontogenetic investigations have not supported this conception. On the one hand, many earlier forms considered gymnocarpous, as *Helvella*, have been shown hemiangiocarpous; on the other hand, in *Ascobolus* gymnocarpous and hemiangiocarpous species appear side by side. Besides the variability of the terms gymnocarpous and angiocarpous lead to abstract difficulties; thus in *Leotia* the sheath is only transitory and disappears before the hymenium is formed. The hymenium is exogenous, as in typical gymnocarpous forms, although the young fructification was surrounded by a hyhal veil.

Hence one is obliged to unite the earlier order of Helvellales and Pezizales, as is done here with the support of Boudier and Durand. The classification of this large new order is accomplished on the biological individuality of the asci. In one series, the Inoperculatae, the asci open, as in the other Ascomycetes, at their tips by an irregular rupture which may close after the exit of the ascospores and be no longer visible. In another series, the Operculatae, they open by the raising of a pre-formed lid (operculum). In addition to this anatomical feature of the asci, these two series differ in histological characters (Lagarde, 1906), which cannot yet be formulated in general terms.

The further classification of the two series is based on the structure of the fructifications. Each series is split into a large number of families on characters of the fructification, of which seven will be discussed in the Inoperculatae, and five in the Operculatae. They are parallel in several respects and, in the higher forms, lead to striking convergence phenomena. As very few of the transitional types have been ontogenetically investigated, the construction of a family tree is not yet possible.

The simpler groups of the Inoperculatae, as the Philipsielleae, the Agyrieae, the Celidiaceae and Patellariaceae, are mostly parasitic or saprophytic on wood, bark or lichens, etc. Morphologically they are very close to many lichen-forming Discomycetes and have therefore often been considered lichens. The fructifications are frequently small and transitory and hence generally known only from hebarium material. In any case, they are connected by numerous intermediate forms with the Plectascales, especially the Gymnoascaceae, and with the Myriangiales, especially the Saccardiaceae, so that they are classified variously by systematists. The Philipsielleae and Agyrieae, especially, have entirely atypical immarginate fructifications whose spherical or ovoid asci are

separated from each other by irregular paraphysoid hyphae intertwined above to a loose, lumpy epithecium (probably the remains of an interthecial stroma) as imperfect stages, free conidiophores, and pycnia are known.

In the higher groups, as the Dermateaceae (apothecia horny or leathery) and Bulgariaceae (apothecia gelatinous), the fructifications are conspicuous and possess a typical apothecial structure. Their disc is covered by a membranous layer which is finally torn and disappears; by this character they are related to the Phacidiales, on one hand to the Stictidaceae whose fructifications, as in the Bulgariaceae, are gelatinous, and on the other hand to the Tryblidiaceae which usually seem deceptively like many Dermateaceae, *e.g.*, certain species of *Cenangium*. The

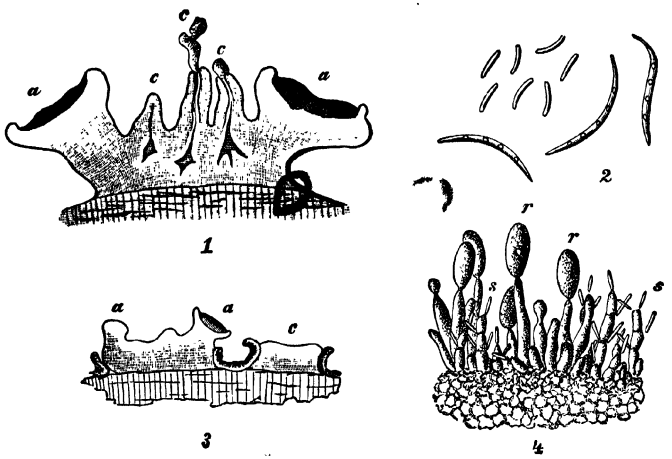


FIG. 209.—*Dermatea Cerasi*. 1. Section of stroma, with apothecia, *a*; conidial cavities, *c*. 2. Macro- and microconidia. *Dermatea carpinea*. 3. Stroma showing apothecia, *a*; conidial fructification, *c*. 4. Portion of conidial fructification of *Dermatella dissepta*, showing bacilliform conidia, *s*; ellipsoidal conidia, *r*. (1 × 10; 2, 4 × 380; *after Tulasne.*)

paraphyses intertwine to a firm epithecium above the tips of the asci in the Bulgariaceae and Dermateaceae (as in many Philipsiellaceae–Patellariaceae and Phacidiales).

Dermateaceae.—Some species of *Dermatea* and *Cenangium* are important plant pathogens. Their several fructifications are erumpent from a poorly developed hypophloedal stroma (Fig. 209); when dry, they form an invisible, usually dark-colored membrane; in moist weather they swell to conspicuous leathery structures. The same stroma bears first conidia, later apothecia. In many forms, as *D. Cerasi*, the conidiophores are united into Valsaceous pycnia (Fig. 209, 1), in others as *Dermatella dissepta* they are free on the substrate (Fig. 209, 4). *Dermatea carpinea* causes a dangerous stem and twig disease of the hornbeam, *D. cinnamomea*, a similar one of oak and *Cenangium Abietis*, one on pines.

Bulgariaceae.—*Bulgaria* and *Coryne* are notable for the remarkable development of their imperfect forms. *Bulgaria polymorpha* (*B. inquinans*) forms circular brown fructifications on the wood or bark of fallen frondose trees. The nuclear divisions in their asci do not take place simultaneously, so that the early and late maturing nuclei compete for the epiplasm (Moreau, 1914). The first-formed spores are normally brown and have a meridianal germination slit; the younger remain hyaline and lack this split (**anisospory**). The species of *Coryne* are mostly saprophytic or hemiparasitic on wood and bark.

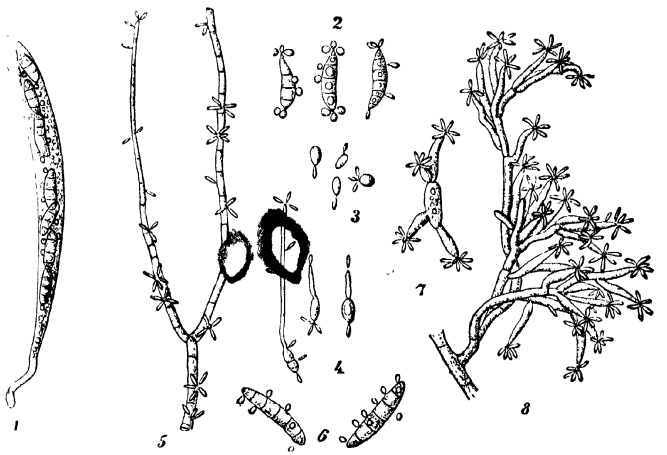


FIG. 210.—*Coryne prasinula*. 1. Ascus whose spores are already forming sprout cells. 2. Discharged ascospores continuing sprouting. 3. Spherical sprout cells which are forming bacilliform cells. 4. Sprouting hyphae. 5. Beginning of conidial formation. *Coryne Cylichnium*. 6. Sprouting ascospores. *Coryne sarcoides*. 7. Germinating ascospore. 8. Conidiophores. (1 to 5, 7, 8 × 350; 6 × 360; *after Brefeld and Tulasne*.)

In both genera the ascospores develop sprout cells in nutrient solutions or mycelium, which in turn may form sprout cells. In *Coryne prasinula*, a form with greenish apothecia on decaying wood, sprouting begins in the ascus (Fig. 210, 1); the several-celled hyaline ascospores develop tiny, spherical sprout cells, and continue to grow after ejaculation (Fig. 210, 2). Besides, they may just as frequently develop to luxuriant hyphal mycelia whose cells cut off on all sides large masses of bacilliform sprout cells. Similar bacilliform cells occasionally sprout from the spherical sprout cells (Fig. 210, 3) or their germ tubes. Both types multiply intensively and in solutions form opaque precipitates, but may at any time, with a change of cultural conditions, proceed to hyphal growth.

Similar relationships have been determined for *Coryne Cylichnium* and *C. sarcoides*, whose large apothecia have a dark flesh-red color, in

which the formation of bacilliform cells on the mycelium is no longer indefinite but limited to the tips of the conidiophores; these arise only when the mycelium has attained a large expanse and by their general rich branching give rise to coremial formation (Fig. 210, 8). In nature these coremial formations have proceeded further to large, irregular, folded conidial layers of the color and consistency of apothecia, whose surface is occupied with conidiophores such as the mycelium produces.

Cyttariaceae.—This monotypic family forms a special type of the stromatic Pezizales. *Cyttaria* is parasitic on species of *Nothofagus* in the



FIG. 211.—*Cyttaria Gunnii*. *a*, twig of *Nothofagus Cunninghami* with fungus galls; *b*, group of stromata; *c*, section of a single stroma. (*a* × ½; *after Berkeley.*)

southern hemisphere and stimulates them to abnormal woody growths. These knobby stromata, in some species brightly colored, generally break out in groups (Fig. 211, *b*); they gelify at maturity and are used by the natives for food. Numerous apothecia arise over the entire stroma under the cover layer (Fig. 211, *c*), and are only liberated at maturity by gelification of this tissue. In *C. Darwini*, the pycnia are found on the stipe in young fructifications, in *C. Harioti* sparsely scattered on the lower side, and in *C. Hookeri* on the apical portion (E. Fischer, 1888).

All these stromatic Pezizales, despite their varied forms and unknown ontogeny form a special side line of the order. In the next groups, without stroma or epithecium, we deal with portions of the order which have been very much investigated cytologically. We will discuss two para-

sitic families, the Mollisiaceae and Helotiaceae, and the saprophytic Geoglossaceae. In the Mollisiaceae and Helotiaceae the peripheral layers are developed to a special peridium; in the Geoglossaceae the hypothecium is homogeneous but differentiated into pileus and stipe; in the Mollisiaceae the peridium is paraplectenchymatic and often built of dark, thick-walled cells; in the Helotiaceae it is prosenchymatic and formed of hyaline, thin-walled cells.

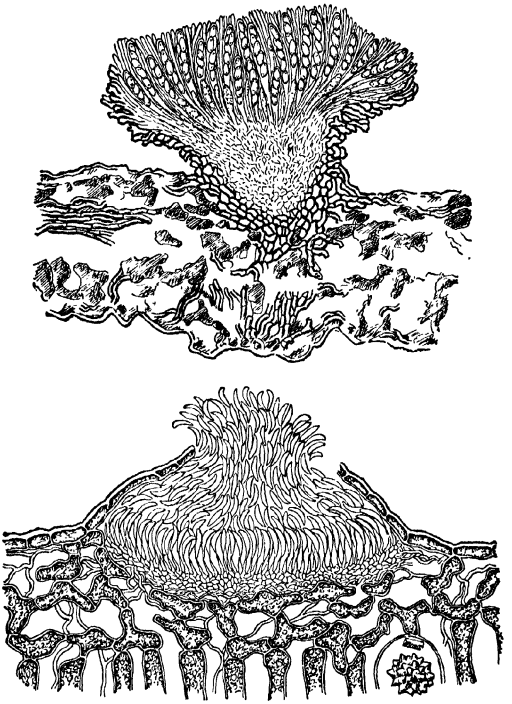


FIG. 212.—*Pseudopeziza Ribis*, *a*, with its secondary spore form, *Gloeosporium Ribis*, *b*. (*After Klebahn*, 1906.)

Mollisiaceae.—*Pseudopeziza* (*Drepanopeziza*) *Ribis* (Klebahn, 1906), causing anthracnose of *Ribes rubrum* and *R. aureum*, from early summer on, produces small brown conidial spots singly or in fused groups 1 or 2 mm. broad, which arise under the upper epidermis of leaves and subsequently raise and rupture it (Fig. 212, *b*). They were earlier described as *Gloeosporium Ribis*. Their spores are colorless, unicellular and sickle shaped, with the thickest spot toward one end rather than in the middle. In damp weather they swell out as light-brown, waxy columns and are generally scattered by rain or insects. They retain their ability to germinate, and possibly to infect, over the whole winter. During the winter,

the apothecia are formed in the interior of the leaves as brown hyphal tangles and break forth during early spring rains. They have a brown peridial layer, 2 to 3 cells thick, which elongates below like a stipe and opens above like a cup.

A similar life cycle has been determined for *Pseudopeziza Medicaginis*, causing a leaf spot of alfalfa, for P. *Trifolii* on clover, forming apothecia even on the living leaves, for *P. tracheiphila* the cause of red burn of the vine and for *Fabraea* (differing from *Pseudopeziza* by multi- rather than unicellular ascospores), *e.g.*, *F. maculata* (*Entomopeziza Soraueri*, *E. Mespili*), the cause of a disease of leaves and fruits of many fruit trees (conidial form *Entomosporium Mespili*), and *F. Fragariae*, the cause of strawberry leaf spot (conidial form *Marssonina Fragariae*).

In other forms, in addition to free conidiophores, pycnia are known, as in *Pezizella Lythri* (Shear and B. O. Dodge, 1921) which causes an early rot of strawberries and other fruits and exits in pathological literature under 27 synonyms: the acervuli as *Hainesia Lythri*, *Sphaeronema corneum* and *Patellinia Fragariae*, etc., the pycnial form as *Sclerotiopsis concava*, *Leptothyrium macrothecium*, *Sporonema quercicolum*, etc.

Only *Fabraea Ranunculi*, on *Ranunculus cassubicus* whose young apothecia form a group of ascogonia with long multicellular trichogynes, has been studied cytologically. Antheridia are lacking (Guseva, 1923). Here are relationships similar to those we shall follow in detail in the operculate forms.

Helotiaceae.—This family, as that of the *Epichloe–Claviceps* series of the Hypocreales, includes two different groups of forms, one (probably simpler) without sclerotia and one (probably higher) with sclerotia. Unfortunately no intermediate forms are known between these two extremes.

Of the stage without sclerotia, may be mentioned *Dasycypha calycina* (*D. Willkommii*), the cause of larch canker. The mycelium of the fungus grows through the bark as a wound parasite and stimulates the cambium to cankerous growths. After the death of the bark these erupt as small, yellowish-white pustules which, in tortuous cavities of their surfaces, form small unicellular hyaline conidia. On the same spot (and also on fallen branches) there later arise orange-colored apothecia.

Sclerotinia is divided into two subgenera, *Stromatinia*, which develops sclerotia in mummified fruit, and *Eusclerotinia* which develops them in root stems or leaves. In the former, the shape of the sclerotia is determined by that of the fruits, in the latter the sclerotia occur in regular weals or callosities.

The more important representatives of the first subgenus are parasitic on fruits of Ericaceae and Rosaceae, *e.g.*, *Sclerotinia Urnula* (*S. Vaccinii*) on *Vaccinium Vitis-idaea*, *S. Ledi* (*S. heteroica*) on *Ledum palustre* and *V. uliginosum*, *S. baccarum* on *V. Myrtillus*, *S. Padi* on *Prunus Padus*,

S. Linhartiana on quinces, *S. fructigena* on apples and pears, *S. laxa* on apricots and *S. cinerea* on cherries, plums and peaches.

In *Sclerotinia Urnula*, the young shoots, infected in the spring, become brown and dry. In their rind, appears a stromatic fungus tissue which sends through the cuticle simple or dichotomously branched conidiophores and cuts off on them moniliform, oidial, citriform, hyaline conidia, smelling like almonds; thus the diseased branches appear mouldy. The conidia were early placed in *Monilia*. At first they cling firmly together with their flat septa. Later these septa split into two lamellae each of which

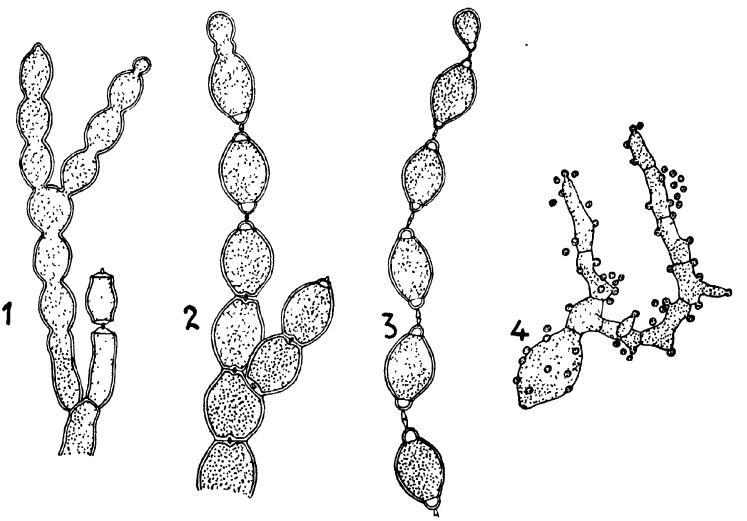


FIG. 213.—*Sclerotinia Urnula*. 1. Young conidial chain. 2. Older stage showing fundaments of disjunctors. 3. Mature conidial chain. 4. Germinating conidium with germ tube beginning to sprout. (× 345; *after Woronin*, 1889.)

detaches in the middle (*mutatis mutandis*, somewhat as in *Albugo*) a small conidial plug (Fig. 213). Both plugs form a fusiform body, the disjunctor. Hence the connection between the conidia has become very loose. When they are touched by insects they cling to them and thus reach the stigmas of their host. Here they germinate to mycelia which, like pollen tubes, penetrate the stylar canals and ovaries, even to the surface of the berries and change them to longitudinally ribbed, brownish, sclerotic mummies. These mummies fall to the ground and winter over. Directly after a thaw, the erupting ascigerous fructification bears an apothecium as broad as 1 to 1.5 cm. on a 2- to 10-cm. long brown stipe, hairy at the base. The ascospores are shot out with great force and, in case they reach the young shoots of the billberry, develop to the above described mycelium.

We find a similar life cycle, especially a similar rhythmic change between moniliform spores provided with disjunctors and apothecial

forms maturing in the overwintering fruit, in the other representatives of the subgenus *Stromatinia*. In the forms on Rosaceae, the conidia are also formed on the fruits (often predominantly on these) so that an infection from fruit may take place. In this manner the fungus may spread extremely rapidly, especially on stored fruit, causing the fruit industry enormous losses.

The change, here described in detail for *S. Urnula*, of an imperfect form developing in spring on the young shoots of a host to a perfect form developing in the course of the summer on the host fruit, has the possibility of a special biological relationship, which has been investigated in *S. Ledi* and *S. Rhododendri*. When in the spring the ascospores of the

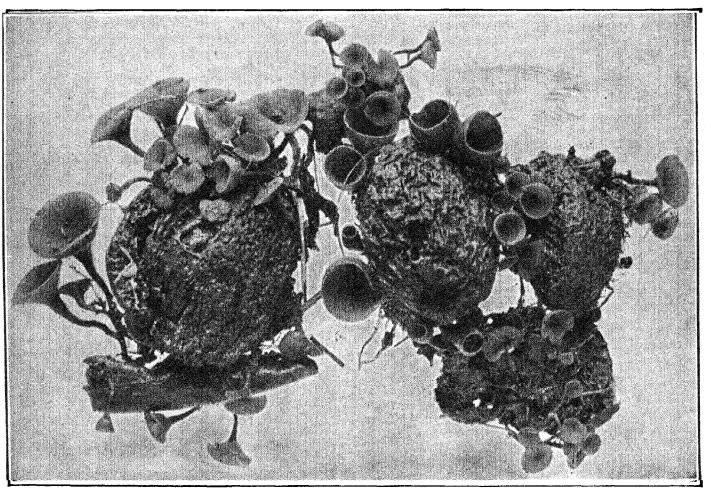


FIG. 214.—*Sclerotinia cinerea*. Apothecia developed in the spring from peach mummies (*Photograph by E. E. Honey.*)

former are mature, *Ledum* is not yet developed; *Vaccinium* is ready, however, to unfold its young shoots. These are infected by the ascospores which develop mycelia in them and form moniliform conidia. Meanwhile *Ledum* has bloomed, the conidia from *Vaccinium uliginosum* infect the ovaries of *Ledum palustre* and here develop the sclerotia with which the fungus overwinters. Similarly, in the spring, *S. Rhododendri* forms its *Monilia* stage on the twigs and branches of *Vaccinium Myrtillus*, while in summer it parasitizes fruits of *Rhododendron* (E. Fischer, 1926). *S. Rhododendri* and *S. Ledi*, as the *Claviceps* on *Brachypodium silvaticum*, in the Hypocreales, need two hosts for the completion of their life cycle; *Vaccinium Myrtillus* and *V. uliginosum* for the imperfect forms and *Rhododendron ferrugineum* and *R. hirsutum* and *Ledum palustre*, respectively, for the perfect forms. Thus they are heteroecious, even if not in

the obligate manner we shall find in the Uredinales. While in the latter the host change is connected with a change of nuclear phase, is conditioned in its rhythm by plasmogamy and meiosis, and, besides, usually takes place between two hosts far removed systematically; in *Sclerotinia* and *Claviceps* we are dealing with plurivorous forms which have been specialized on seasonal hosts.

The economically important representatives of the subgenus *Eusclerotinia*, as *S. Fuckeliana*, *S. Libertiana*, *S. Trifoliorum* and the various Sclerotinias on monocotyledonous bulbs, in their choice of hosts are much less specialized than those of the subgenus *Stromatinia*. Thus, *S. Fuckeliana* is parasitic on the Vine, *Ribes*, turnips, etc., *S. Libertiana* on all sorts of cultivated garden vegetables and *S. Trifoliorum* on alfalfa,

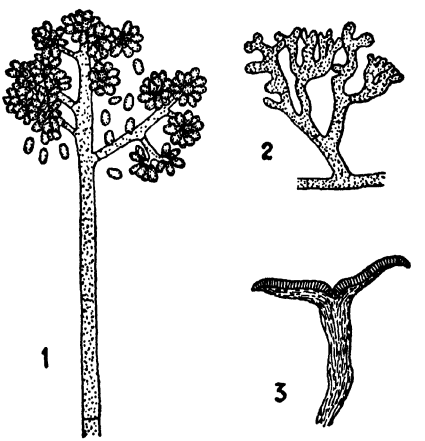


FIG. 215.—*Sclerotinia sclerotiorum*. 1. Conidial stage. *Botrytis cinerea*. 2. Appressorium. 3. Diagrammatic cross section of apothecium. (*After R. E. Smith*, 1900.)

Onobrychis sativa, clover, etc. During the summer, they kill the infected organs, developing in them the sclerotia in which they overwinter. Their conidia arise singly on characteristically formed conidiophores (Fig. 215, 1) and hence, in contrast to those of *Stromatinia*, are placed in *Botrytis* rather than in *Monilia*. As the cultural determination of the perfect form is rarely possible, one generally places them, especially those of the *S. Fuckeliana* and *S. Libertiana* groups, in the collective species *Botrytis cinerea*. Thus one provisionally names all entirely or hemiparasitic pathogens which probably belong in the life cycle of a *Sclerotinia*.

Kharbush, (1927) reports the usual nuclear phenomena in the development of the ascogenous hyphae and asci in *Sclerotinia Fuckeliana*.

Geoglossaceae.—While in the Mollisiaceae and Helotiaceae the fructifications have the typical apothecial structure, in the last family of the Inoperculatae, the Geoglossaceae, there appears a fundamental

change. The young stages of their lower forms connect directly to the higher forms of both these families, which lack sclerotia and generally are tough, fleshy or leathery, but gelatinous in some Cudonieae, as in the Bulgariaceae. Since there appears a strong epinastic growth of the top of the hypothecium, however, the ascus hymenia are not longer formed in the interior of patelliform or cyathiform fructifications but on the convex exterior of clavate fructifications.

This may be best followed in a very simple example, *Roesleria pallida* (*Calicium pallidum*) on the roots of the Vine. Its fructification consists of a coremial hyphal tuft which is differentiated into a stipe and a flat

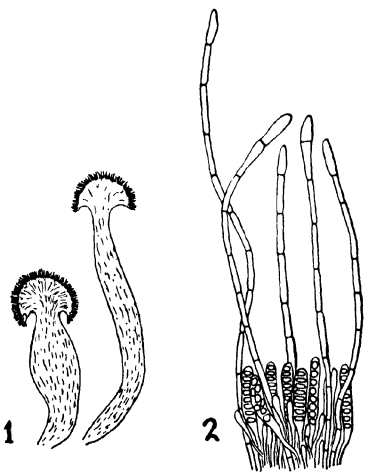


FIG. 216.—*Calicium pallidum* (*Roesleria pallida*). 1. Section of fructifications. 2. Portion of hymenium showing asci and paraphyses. (1 × 8; 2 × 320; *after Arnaud*, 1912.)

discoid head (Fig. 216, 1). If we imagine this disc curved like an urn, as it is in *Caliciopsis*, a related genus, we have before us a true apothecium of about the height of an Agyrieae–Pattelariaceae group. If we imagine the hypothecium more strongly developed, so that the subhymenial layer arches convexly, we have one of the simplest Geoglossaceous fructifications represented in Fig. 216. The extremely primitive position of *Roesleria pallida* is further shown by the fact that its asci mature at different times, so that while the old asci discharge first uni- then bicellular ascospores, the hymenia continually form new asci.

In the higher Geoglossaceae this arching of the hypothecial tip goes still further and leads to a clavate outline of the fructification as shown in Fig. 217 for *Gloeoglossum glutinosum;* in it the whole club is fertile, *i.e.*, covered by an ascus hymenium. At times, as in *Geoglossum difforme*, this hymenium may extend over the whole stipe.

In the course of the further development, the fertile portion becomes increasingly separated from the sterile and changes to pileate head; this head is fertile only on its upper side, however, while the lower remains sterile. The forms with the originally clavate fructifications are united in the subfamily Geoglosseae, those with capitate fructifications in the Cudonieae. Their classification rests on the special differentiation of these fructifications and on the form of the ascospores and paraphyses. To the Geoglosseae belong *Mitrula, Microglossum, Geoglossum, Gloeoglossum, Trichoglossum* and *Spathularia;* to the Cudonieae, *Leotia* and *Cudonia* (Durand, 1908).

As far as the ontogeny of the Geoglossaceae has been studied, about one-half the forms correspond to the normal hemiangiocarpous type, the other half to the purely gymnocarpous. To the former there belong *Spathularia velutipes, Cudonia lutea, Microglossum viride* (Duff, 1920, 1922) and *Mitrula paludosa* (*M. phalloides*) (Dittrich, 1902). To the second group belong *Trichoglossum hirsutum, T. velutipes, Geoglossum glabrum* and *Gloeoglossum difforme* (Duff, 1920, 1922). While the hemiangiocarpous type includes all possible forms, the gymnocarpous forms are closely related and grouped around *Geoglossum.*

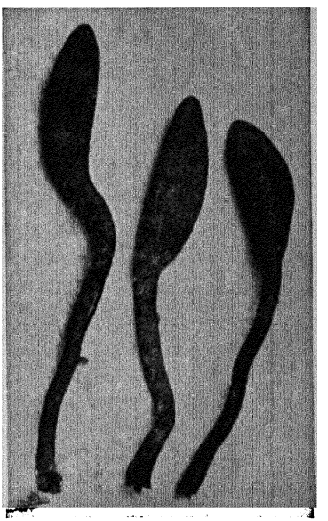


FIG. 217.—*Gloeoglossum glutinosum.* (Natural size; *after Falck*, 1916.)

In youth, the fructifications of both groups seem identical. They arise as a tangle of closely twined hyphae which are elongate at the periphery and entirely surround the tangle. In the middle of the base, however, they are more rounded or polyhedral. The middle cells elongate upwards and thus cause the elongation of the whole fructification, while the basal cells remain irregularly angular with thickened walls. In the hemiangiocarpous group the peripheral hyphae, six to eight cell layers deep, gelify and surround the whole fructification in a gelatinous sheath which in systematic literature is called veil or volva; it corresponds to the velum universale of the Agaricales (*mutatis mutandis*). In most forms it remains one layered; in *Spathularia velutipes* it divides into a compact, thin-walled, inner and a loose, thick-walled, outer layer. In the gymnocarpous group, there is no differentiation of a special sheath layer and the fructification is open throughout its whole development.

In the apical parts of the fructification, the hyphae underneath (or in the gymnocarpous forms, those directly under the surface) become

arranged in a palisade and develop to paraphyses. By the pressure of the growing paraphyses, the sheath is ruptured, allowing the apical portion to project. Finally the ascogenous hyphae push from the ground tissue and form asci. In certain species, *e.g.*, *Cudonia lutea*, the tearing of the veil may come very late when many asci are already mature.

The sexual organs of the Geoglossaceae undergo a peculiar degeneration, such as we shall meet again in the Lecanoraceae–Cladoniaceae (*Icmadophila–Baeomyces*) series. As in the latter, the ascogonia do not arise directly from vegetative hyphae but from a loose tangle of densely staining hyphae, the so-called generative or primordial hyphae.

In the first stage, as in *Leotia gelatinosa* (*L. lubrica*), they form one (or several) ascogonia at the base of the fructification (Dittrich, 1902; Brown, 1910, Duff, 1922) very early, when the fructification is a small, undifferentiated tangle. Nothing is known of their form. It was observed, however, that from a single large cell, the ascogenous hyphae develop *pari passu* with the elongation of stipe and finally form asci between the paraphyses. In analogy to the Operculatae, one may assume that this one large cell is the privileged sexual cell of the ascogonium and that the sexual act is probably parthenogamous.

In the second stage in *Cudonia lutea*, the formation of ascogonia is retarded. Here the generative hyphae are early differentiated before the volva is formed. They remain inactive, however, in the apical zone of the fructification several cell layers below the later paraphyses and are raised by the central hyphae, on the elongation of the fructification. At a given time, they grow out into the ground tissue of the head and form a large number of slightly curved or helical, at first uninucleate, later multinucleate ascogonia which open out into typical multicellular trichogynes; these penetrate the veil and project a distance into the open but degenerate early. Antheridia are lacking; the nuclei in the ascogonia are arranged in pairs and migrate into the ascogenous hyphae. Thus the sexual processes are autogamous.

In *Spathularia velutipes*, not only the formation of ascogonia, but also that of generative hyphae is retarded, and they only appear when the fructification attains a considerable size; here also they lie directly under the tip and, as in *Cudonia lutea*, develop to ascogonia. These are morphologically quite degenerate, however, and no longer possess trichogynes (Fig. 218, 1); they differ from the usual vegetative hyphae of the hypothecia only in their greater cross section and deeper staining. Their nuclei also pair and migrate into the ascogenous hyphae.

Finally, in the fourth stage, in *Trichoglossum hirsutum*, the sexual organs are no longer morphologically recognizable as such. Neither generative hyphae nor ascogonia are formed and the ascogenous hyphae develop in some unknown manner from any vegetative hyphae rich in protoplasm.

In the Geoglossaceae so far known the antheridia have completely disappeared and, consequently, the ascogonia develop autogamously. They undergo a gradual degeneration: at first they possess a typical form and a well-developed trichogyne, then the typical form is lost, along with the trichogyne, and finally they are no longer formed and the development of the ascogenous hyphae takes place pseudogamously.

In contrast to the previous families, imperfect forms are still unknown in the Geoglossaceae on account of their saprophytism on decaying wood, etc.; in *Spathularia* and *Cudonia* it has been noted that the ascospores

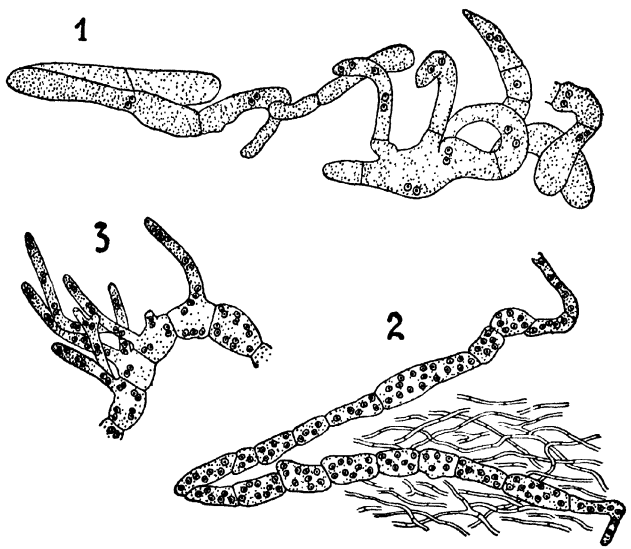


FIG. 218.—*Spathularia velutipes*. 1. Ascogonium with ascogenous hyphae. *Rhizina undulata* 2. Young ascogonium. 3. Development of ascogenous hyphae. (1 × 1,330; 2, 3 × 335; *after Duff*, 1922, *and Fitzpatrick*, 1918.)

(as also in the Dermateaceae in *Tympanis* and in the Patellariaceae in *Biatorella*) may germinate to a sprout mycelium while still in the ascus.

In summary, the Inoperculatae are an entirely indefinite mixture of various poorly known genera which will only be arranged in clearer lines after more detailed ontogenetic investigations. Apparently the lower forms connect directly to the Plectactascales and Myriangiales and perhaps properly belong there. As long as their ontogeny is unknown, however, an approach to the understanding of the Inoperculatae and the Discomycetes in general is closed to us.

On the other hand, we are comparatively well informed on the ontogenetic relationships of the Operculatae, in any case in the lower forms. They are here described for only the five more important families, the Rhizinaceae, Pyronemaceae, Ascobolaceae, Pezizaceae and Helvellaceae.

The Rhizinaceae and Pyrenemaceae form the gymnocarpous stage; the former ascend from simple, loose layers to tuberous, tortuous fructifications, the latter develop to typical apothecia of the Pezizales.

Rhizinaceae.—The lowest stage is *Ascocorticium* whose representatives form thin membranes of whitish or reddish color on bark, etc., such as we shall meet in the Corticiaceae of the Basidiomycetes. On these coverings, there is laid an even hymenium of eight-spored asci without paraphyses. Perhaps the curious *Medeolaria Farlowi* on *Medeola virginiana* belongs here. The indeterminate hymenium spreads over the epidermis of the host, producing many fascicles of paraphyses but few asci with dark brown, striate spores (Thaxter, 1922). Unfortunately the ontogeny of these forms is not yet known.

A higher stage is taken by *Rhizina*, whose original flat fructifications, later generally arched upward, have the consistency of fleshy crusts. *R. undulata* forms luxuriant white mycelia on the roots of many forest trees. Later these intertwine on the roots or on the earth to small hyphal tangles whose peripheral ends show a tendency to form a palisade, later a paraphyseal layer. When these knobs have attained a cross-section of about 1 mm., as many as eight ascogonia form in their interior. From the beginning, these are multinucleate and arise from ordinary vegetative hyphae. These wind loosely through the other hyphae and consist of ten to nineteen or more cells (Fig. 218, 2). The terminal cell is small and pointed; its content is early disorganized; possibly it is a functionless trichogyne. When the ascogonia have matured, large pores are formed in the septa so that the cells come into open communication with each other. About half of the cells, chiefly those which lie in the middle of the ascogonium, develop now into ascogenous hyphae (Fig. 218, 3) into which flows the protoplasm of the remaining basal cells (Fitzpatrick, 1917, 1918).

The highest stage is shown by the *Sphaerosoma* group (Rouppert, 1909; Setchell, 1910) whose fructifications are generally hidden in the forest between dead leaves and, on account of their tuberous form and fleshy mass, are often considered truffles. Their earliest stage corresponds in structure to the simple apothecial scheme (Fig. 219, 1). Then, however, the hymenium develops very strongly towards the sides, consequently the edges of the cup arch downwards and often form an indented, folded, hollow sphere up to 3 cm. in diameter, which in *S. fuscescens* (*S. Janczewskianum*) and *S. echinulatum* show their origin from a stipe (Fig. 219, 2). The hymenium develops hemiangiocarpously on the exterior of this hollow sphere (while the interior remains a sterile hypothecium) and consists of asci and paraphyses, which latter often intertwine over the tips of the asci. In the closely related *Sphaerozone ostiolatum* (*Sphaerosoma fragile*), having verrucose instead of echinulate spores, development has been reported as gymnocarpous. In another

closely related genus, with reticulate spores, *Ruhlandiella berolinensis* and *R. hesperia*, the paraphyses form a gelatinous epithecium which is persistent at maturity, while the hypothecium is poorly developed.

The highest member of this series is *Mycogalopsis retinospora* (Gjurašin, 1925) which superficially is very close to *Ruhlandiella* and perhaps should be referred to that genus. Here the hymenium is covered with a layer of plectenchyma until maturity, suggesting the conditions found in the Tuberales. The presence of a thin, more or less evanescent subiculum (also found in *Ruhlandiella*) and the well-developed stalk suggest their relationship to the *Sphaerosoma* group, while the breaking away of

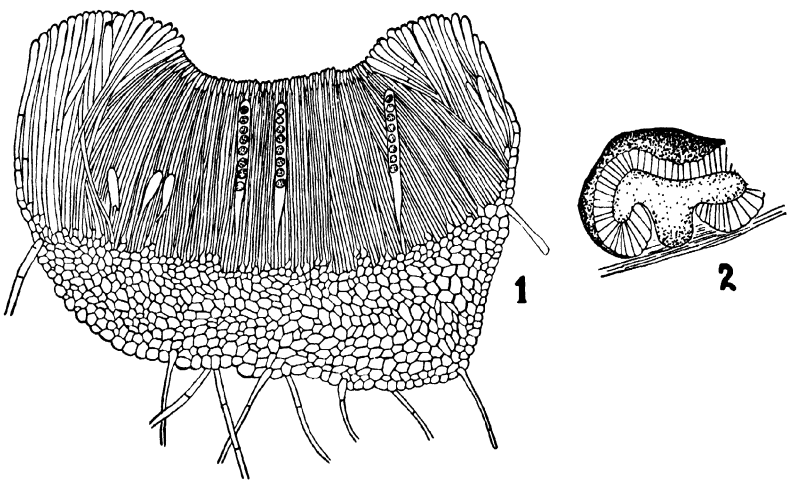


FIG. 219.—*Sphaerosoma fuscescens*. 1. Section through a very young fructification. 2. Diagrammatic section of an old fructification. (1 × 67, 2 × 4; *after Rouppert*, 1909.)

the covering of the apothecium, leaving a dusty mass of yellow spores, suggests conditions seen in *Myriangium*.

The ascus stroma develops rapidly on rabbit dung, maturing in about a week. Three to six, three- to four-nucleate ascogonia arise at a point on the subiculum, grow perpendicular to it and are abjointed. No antheridium was observed. The ascogonia are soon surrounded by a thin peridium developed from neighboring hyphae. Ascogenous hyphae develop from the ascogonia forming asci directly on the tips of the branches while the paraphyses develop from the cells immediately below the ascogonia. Nuclear fusion in the ascus and subsequent spore formation is normal.

Thus in this family we have a transition from a simple hyphal subiculum of unlimited growth and a gymnocarpous formation of the hymenium to a highly developed, more or less tuberous ascocarp, with angiocarpous

development very suggestive of the Tuberales; hence in that order we shall return to this series.

Pyronemaceae.—The significance of this family does not lie in its fructifications, but in the relationships of its sexual organs. They form an extremely primitive group and include forms which are lower than any of the previously discussed types of the Inoperculatae. Their fructifications rest on single hyphae or hyphal tissues, and are merely loose, open, immarginate, ascigerous discs, penetrated by paraphyses. Sometimes one consists of a tuft of asci resting upon a more or less well-developed hypothecium. Only two genera will be discussed here: *Pyronema*, morphologically higher with a well-developed hypothecium, and *Ascodesmis*, morphologically simpler with poorly developed or almost no hypothecium. An idea of *Pyronema* may be derived from the figure of *Sphaerosoma fuscescens* (Fig. 219, 1), if one imagines the apothecial margin absent so that the ascigerous hymenium, as in the Phillipsielleae and Agyrieae, covers the whole top of the hypothecium. Figure 223, 5 shows *Ascodesmis;* if one imagines this ascus tuft laid on or in a loose subiculum, one has a cross section through one of the Gymnoascaceae.

Pyronema confluens, the best known representative (Harper, 1900; Dangeard, 1907; Kosaroff, 1907; Claussen, 1912), is gregarious on the bottom of damp piles of charcoal, occasionally on pots of sterilized earth, and forms there its lenticular, 1 to 3 mm. broad, flesh or rose-red fructifications (apothecia) which are generally confluent in groups (hence the species name) resting upon fine hyphal tissues.

The hyphal cells are multinucleate. At the formation of the fructification one, more rarely several, hyphae fork repeatedly and grow upwards so that small tufts of rosettes result. Originally this whole branching system is unicellular. Later the single multinucleate branches are abjointed. Such an abjointed uninucleate, cellular branch (the later ascogonium) attains a thick, clavate structure and, while at its base one or two stipe cells are formed, its tip elongates to a multinucleate papilla, the later trichogyne. Subsequently, its lower end is abjointed from the swollen ascogonium beneath (Fig. 220, 1).

In the immediate vicinity of the ascogonial branch and on the same hypha there arises an antheridial branch (and this occurs very early) in which the first contact of the two organs stimulates branching, such as has just been described for the female organ. The female branches are always somewhat ahead of the male in development. Finally, in the latter, the multinucleate end cells and one or two stipe cells are abjointed from the hypha and develop to clavate antheridia (Fig. 78).

During the further development, the nuclei in both antheridia and ascogonia increase much in size; those of the trichogynes, however, remain small and gradually degenerate (Fig. 220, 2). Both in antheridium and ascogonium, a few nuclei degenerate before plasmogamy. The

number of female nuclei in each ascogonium always reaches several hundred. The male nuclei group into a thick protoplasmic mass in the vicinity of the tip of the trichogyne; the separating membrane is dissolved and they migrate into the trichogyne (Fig. 220, 3). Meanwhile, the female nuclei in the ascogonium have been united to a central hollow sphere, the septum in the trichogyne neck is temporarily dissolved, the male nuclei migrate into the ascogonium and there, for the most part, pair with the somewhat larger female nuclei.

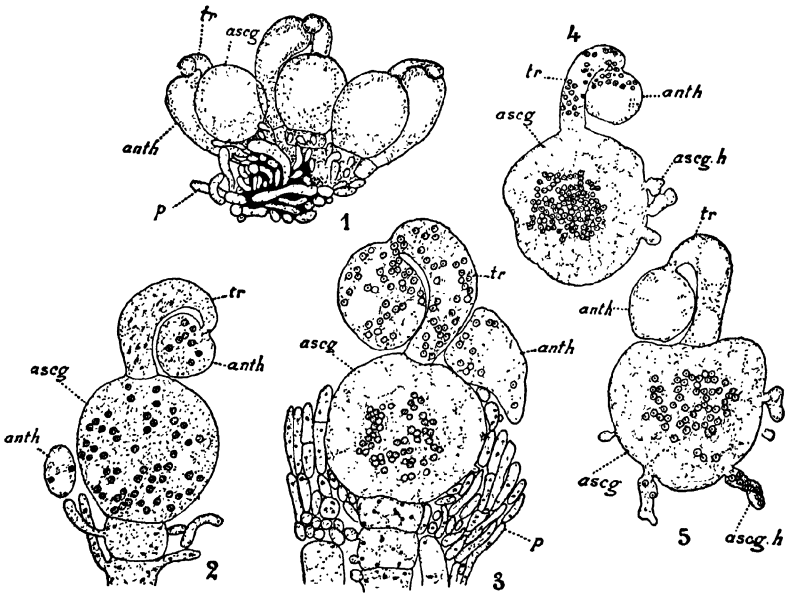


FIG. 220.—Development of sexual organs of *Pyronema confluens*. 1. Tuft of ascogonia, *ascg*, with trychogyne, *tr*, and antheridia, *anth*; *P*, sterile hyphae. 2. The nuclei of the trichogyne degenerate; the antheridium is in open communication with the trichogyne. 3. The male nuclei migrate into the trichogyne; *P*, sterile hyphae which will develop the paraphyses. 4. The basal wall of the trichogyne disappears, the male nuclei migrate into the ascogonium which is already beginning to produce ascogenous hyphae, *asc. h*. 5. The basal wall of the trichogyne again formed; nuclear pairing is completed and several dicaryons have migrated into the ascogenous hyphae. (*After Harper*, 1900.)

After a few hours, ten to twenty ascogenous hyphae grow out of the ascogonium and take up the dicaryons (Fig. 220, 5). They branch very much and the dicaryons increase by conjugate division (Fig. 221, 1). Finally the ascogenous hyphae are broken up by septa so that two to eight dicaryons are present in the vicinity of the ascogonium, and at a distance from it, only one is present (Fig. 221, 2). Which nucleus of the pair is female and which is male is not determinable, as their size differences have disappeared.

The cell with a single dicaryon develops sidewise, with conjugate division of its nuclei, in a hook-shaped process which was described in the introduction to the Ascomycetes as a transitory hook tuft (Fig. 79), and finally forms eight-spored asci. This tuft-like branching of the ascogenous hyphae is one of the grounds for the conical widening which the older fructifications of the Pyrenomemaceae and many other Discomycetes often show.

Already at the time of copulation the sexual organs are surrounded by a loose layer of sheath hyphae. Later, these branch very much, while the sexual organs are crushed and resorbed, and form the paraphyses between which later the asci penetrate (Fig. 222).

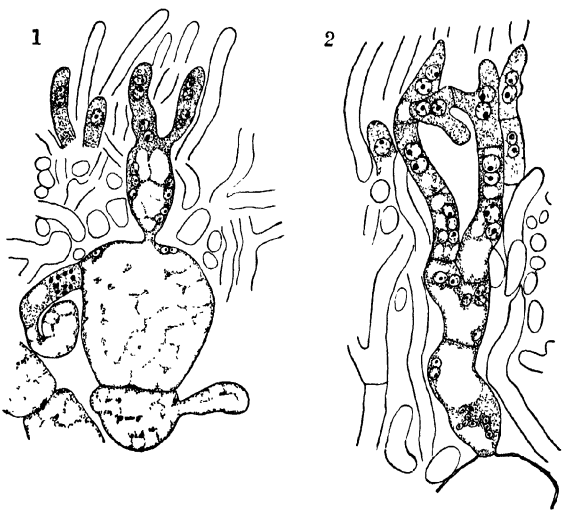


FIG. 221.—*Pyronema confluens*. Development of ascogenous hyphae. 1. The ascogenous hyphae are aseptate and have numerous dicaryons. 2. Development of hooks. (*After Claussen*, 1912.)

In *P. domesticum* (Tandy, 1927) the first and often the third division in the ascus is a meiosis; both diploid and tetraploid nuclei being found in the young ascus. The development of this species follows closely that reported by Harper for *P. confluens*.

The sexual development of *Pyronema* is connected directly to that of *Monascus* among the Plectascales. As there the female sexual apparatus is divided into a unicellular ascogonium and an unicellular trichogyne, and as there is a plurality of sexual acts, there follows a multiple plasmogamy between the male and female gametangial nuclei. It is nevertheless characteristic of *Pyronema confluens* (and the Pezizales generally) that its ontogeny can take place in this manner only when definite nutritive relations occur. If these are absent, the antheridium still may be formed

but is no longer functional or it may be absent. In *Pyronema confluens* var. *inigneum* (Brown, 1915), even under the most favorable conditions, fusion no longer occurs between antheridium and trichogyne, although

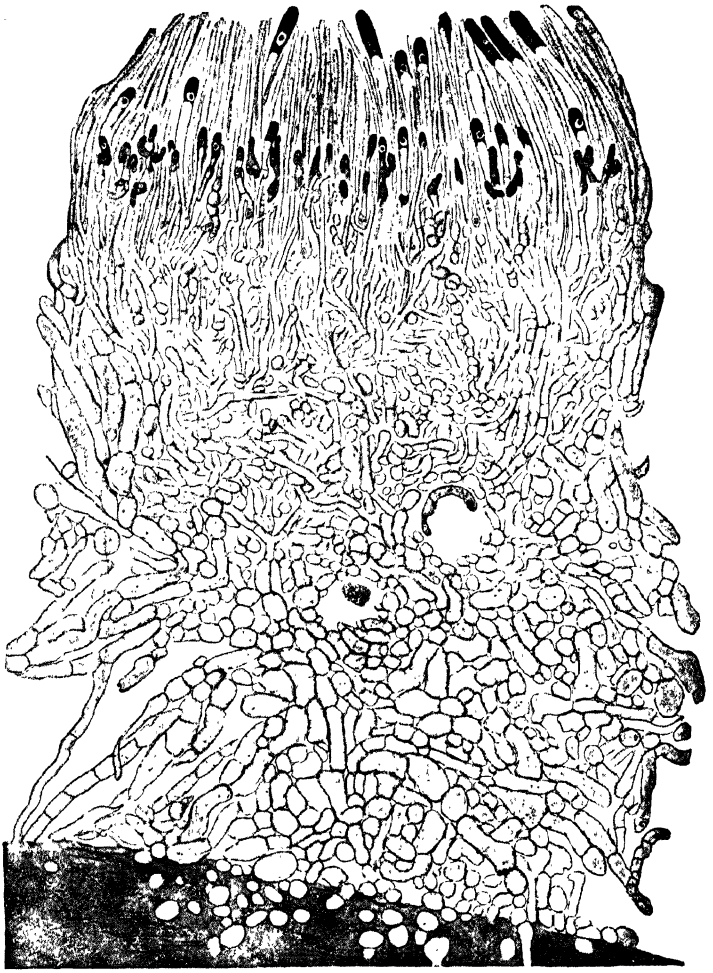


FIG. 222.—*Pyronema confluens*. Section of an almost mature fructification. The ascogonium has collapsed. At the top of the fructification, the ascogenous hyphae have penetrated between the paraphyses and formed asci. Only in the apical portion of the fructification may they be distinguished from the haploid hyphae. (× 290; *after Claussen*, 1912.)

the trichogyne wraps itself around the antheridium several times. In both cases the female nuclei form dicaryons autogamously in the ascogonium and migrate normally into the ascogenous hyphae. The amphi-

mictic sexual act is no longer obligatory for *Pyronema confluens*, but is facultative; its presence or absence and the necessary compensation by autogamy depends only on nutritive relationships.

In contrast to *Pyronema*, the second genus, *Ascodesmis* (Claussen, 1905; Dangeard, 1907), is connected ontogenetically to the *Amauroascus–Aphanoascus* type of the Plectascales. *Ascodesmis nigricans* (*Boudiera Claussenii*) is coprophilous on rabbit dung. In the development of fructifications, a thick branch on any hypha is raised perpendicular to the substrate and after a short time attains a T shape by forking (Fig.

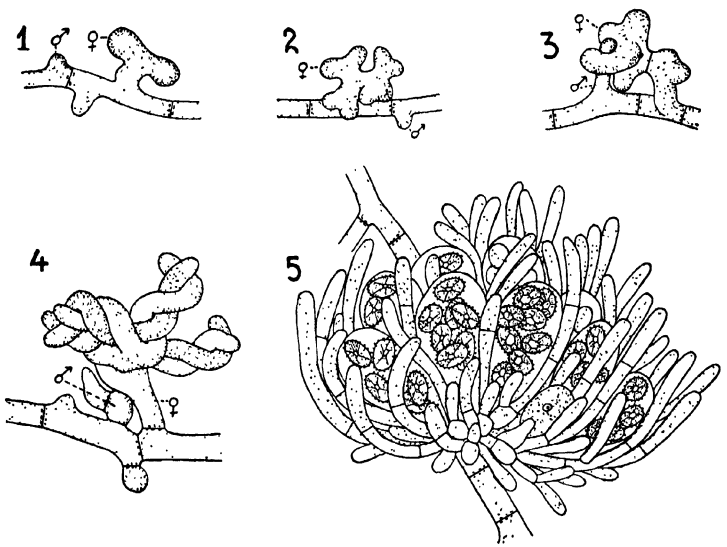


FIG. 223.—*Ascodesmis nigricans*. Development of fructifications. 1 to 4. Development of sexual organs. 5. Young fructification, slightly compressed. (1, 3 × 670; 2 × 540; 4 × 860; 5 × 380; *after Claussen*, 1905.)

223, 2). Each bar of the T forks in a parallel plane near the substrate twice or more, so that finally there arises a structure shown in Fig. 223, 3. This structure (multinucleate) is called **gynophore** (Lotsy, 1907). It is abjointed from the hypha and subsequently develops to numerous helical ascogonia which in turn are abjointed.

In their vicinity, from the same original hypha are one or more branches (**androphores**) forking to form antheridia which subsequently coil helically around the ascogonia. Thus there are formed structures shown in a simple case in Fig. 223, 4.

The antheridial branch (approximately quinque nucleate) remains undivided; the female branch is septate and divides into a short bi- to trinucleate, apical trichogyne, and a longer, about quinque nucleate, **ascogonium.** Hereupon, apparently as in *Pyronema confluens*, after the

degeneration of the trichogyne nuclei, an open communication forms between the two groups of organs, the male nuclei migrate through the trichogyne into the ascogonium which develops in the usual manner to ascogenous hyphae.

Meanwhile the gynophore below the ascogonia develops sterile sheath hyphae which surround the sexual organs and later support the loose apothecia (Fig. 223, 5). They serve in addition, as *Pyronema*, for the nourishment of the growing asci as the reserve materials in their end branches (the paraphyses) disappear at the maturity of the asci.

As in *Pyronema confluens*, so also in *Ascodesmis nigricans*, the male nuclei may degenerate prematurely in the antheridium. In this case amphimixis is absent and the female nuclei pair autogamously in the

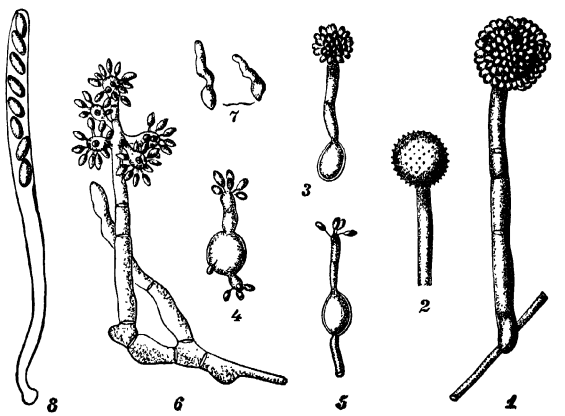


FIG. 224.—*Pustularia vesiculosa*. 1. Conidiophore from mycelium. 2. Tip of conidiophore after discharge of spores. 3 to 5. Ascospores and germ tubes developing directly to conidiophore. *Plicaria repanda*. 6. Branched conidiophores. 7 Germinating conidia. 8. Mature ascus. (1 to 6 × 200; 7, 8 × 240; *after Brefeld.*)

interior of the ascogonium and migrate into the ascogenous hyphae, as in cross-fertilized ascogonia. Thus amphimixis is no longer obligatory but facultative and, according to external conditions, may be replaced by autogamy.

The hemiangiocarpous Operculatae connect through the Ascobolaceae and Pezizaceae directly to the Pyronemaceae. These two families differ from the Pyronemaceae in the higher development of their fructifications. The hypothecium is no longer homogeneous as in *Pyronema*, but is differentiated into a fleshy, occasionally colored peridium and a true ground tissue, the hypothecium. Similarly the hymenium is no longer, as in the Pyronemaceae (insofar as the latter possess a hymenium), open and convex but typically concave, patelliform and, in most forms, angiocarpous. Naturally the transition from the Pyronemaceae is only gradual. In the Ascobolaceae a few forms are still known, *e.g.*, *Ascobolus stercorarius* (*A.*

furfuraceus) and *A. magnificus*, which develop gymnocarpously like the Pyronemaceae.

Furthermore, for the Ascobolaceae–Pezizaceae group various imperfect forms have been reported, while these appear to be absent in the Pyronemaceae. Thus *Ascobolus denudatus*, *A. citrinus* and *Lasiobolus pulcherrimus* have oidia, *A. carbonarius* small conidia on hyphal branches, others, chiefly the forms of Pezizaceae, have true ample conidiophores; in *Pustularia vesiculosa*, *Aleuria asterigma*, (*Peziza asterigma*), *Plicaria ampliata* and *P. repanda*, these conidiophores appear like those of the

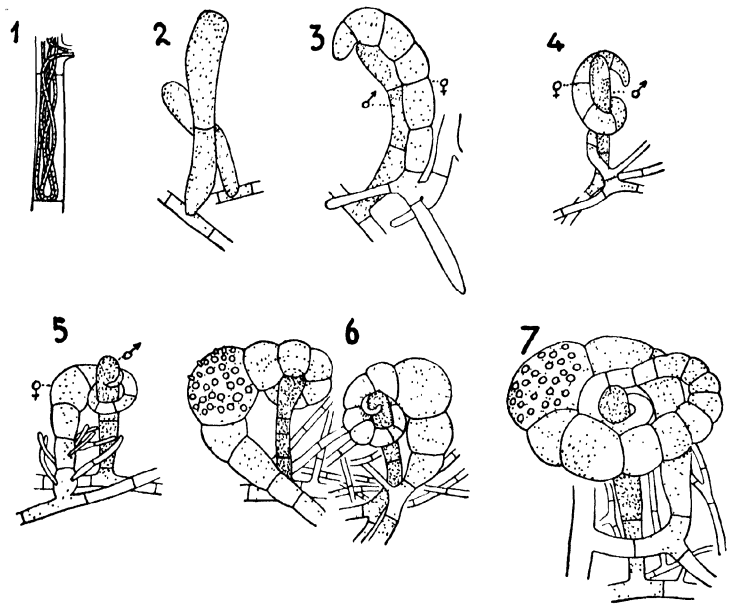


FIG. 225.—*Ascobolus magnificus*. Development of sexual organs. 1. Peculiar proliferation of hyphae. 2. Formation of sexual organs. 3 to 5. Types of copulation. 6, 7. Beginning of ascogenous hyphae. (*After B. O. Dodge*, 1920.)

Zygomycetous *Syncephalis* and the Polyporaceous *Fomes annosus*, and are swollen terminally to small heads which cut off simultaneously hyaline ovoid conidia on short sterigmata; in *Lachnea abundans*, (*L. cretea*), they correspond rather to the *Botrytis* type (B. O. Dodge, 1922; [Fraser] Gwynne–Vaughan and Williamson, 1927). *Ascobolus magnificus*, as in species of *Melanospora*, produces bulbils which correspond to the imperfect, *Papulaspora*.

Ascobolaceae.—The ontogeny of both the Ascobolaceae and Pezizaceae connects directly to the Pyronemaceae and continues the tendencies described for this family. Thus the sexual organs of *Ascobolus vinosus* and *A. macrosporus* (Schweizer, 1923) agree entirely with those of

Ascodesmis nigricans, while *Lasiobolus* (*Cubonia*) *brachyascus* have unicellular ascogonia and trichogynes, like *Pyronema confluens* (Satina, 1921). The antheridium is multicellular, coiling helically about the trichochyne with which it copulates. In still other species have been found developmental forms for which there are at present no parallels in the Pyronemaceae but for which we find complete and significant analogies in the Plectascales. Thus in *Thelobolus Zukalii* and some species of *Rhyparobius* (Ramlow, 1915), the antheridia and ascogonia twine helically, as in *Penicillium crustaceum*. In *Ascobolus magnificus* (B. O. Dodge, 1920), finally, the morphological relationship is reminiscent of *Amauroascus*. This species is interesting because it is heterothallic. Single spore cultures do not produce apothecia; these appear shortly if the complementary mycelium is present.

Four to six days after the sowing, there appear on the hyphae short, clavate, one- to two-celled branches which stand vertically from the substrate. In a few hours they increase considerably in length; one branch, the antheridium, usually remains vertical; the ascogonium, if it is in the immediate vicinity coils about the antheridium (Fig. 225, 3) or, if it is further away, its tip grows toward and coils about the antheridium (Fig. 225, 4 and 5). In both cases the trichogyne comes into open communication with the antheridium, whereupon the ascogenous hyphae grow out of a cell nearer the base (Fig. 225, 6 and 7). All these types, however different their external forms, have in common a well-developed amphimixis which, at least in *Ascobolus magnificus*, shows a physiological sexual differentiation, heterothallism.

In numerous other forms, there appear successively all sorts of degeneration phenomena such as are numerous in previously described Ascomycetes: the antheridia disappear and in place of the original amphimixis, appear various kinds of deuterogamy; at first a modified amphimixis, for which no term exists (*Ascobolus carbonarius* type), then parthenogamy, in which cell fusion occurs between two female sexual cells, then autogamy in which cell fusion is absent and nuclear pairing occurs within a single sexual cell and finally pseudogamy (at least in the Pezizaceae) in which vegetative hyphae copulate.

Ascobolus carbonarius is one of the theoretically most important forms of fertilization of the higher Ascomycetes because it facilitates an understanding of sexuality of the lichens. The ascogonium, in the absence of antheridia, grows toward conidia, surrounds them and apparently copulates with them. Thus Fig. 226, 1 shows a stipitate ascogonium, surrounded by sheath hyphae, which itself has arisen directly from the germ tube of a conidium C_1; it has formed toward the left a very long trichogyne which then surrounds another conidium C_2. Hereupon the ascogenous hyphae grow from some basal cell of the ascogonium. The ascogonium in Fig. 226, 3, showing such a relationship, has ceased develop-

ment. Furthermore, without copulation the ascogonia seem to be able to continue their development parthenogenetically. The ascogenous hyphae of *Ascobolus carbonarius* show a marked separation into a primary and a secondary phase, as in *Pyronema confluens* (p. 130) and in the Plectascales. The ascogenous hyphae which bud directly from the ascogonia are vertical and at first unbranched. Later their ends branch to secondary hyphae which subsequently proceed to the formation of hooks and asci in the usual manner.

Ascobolus carbonarius is the only known example in the Pezizales where a sexually active ascogonium, in the absence of antheridia, copulates with vegetative structures in order to draw from them the necessary foreign nuclear material. Thus it is characteristic for its double position

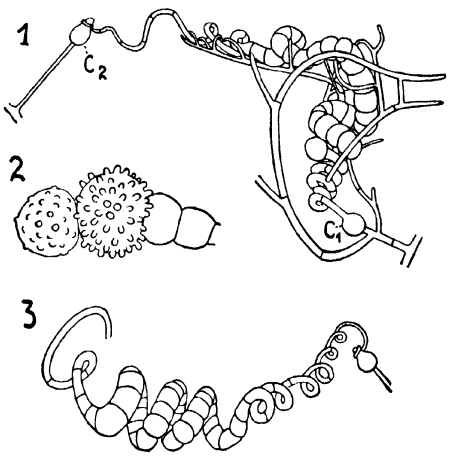


FIG. 226.—*Ascobolus carbonarius*. Development of ascogonia. (× 265; *after B. O. Dodge*, 1912.)

that, on the one hand, the ascogonia are still adjusted for cross fertilization, while on the other hand, the antheridia have disappeared, so that this cross fertilization may only occur by a substitute. It is also characteristic that this cross fertilization, as in the Pyronemaceae, is not obligatory but that when it is absent the ascogonia may develop independently. It is also noteworthy that this species is heterothallic (Betts, 1926). Single spore cultures fail to produce apothecia. This sexual differentiation takes place in the ascus, since cultures from the spores of a single ascus gave equal numbers of + and − mycelia.

This cross fertilization, since of the numerous forms studied only *A. carbonarius* shows the transitional type, appears to have been rapidly lost or is only realized in a few cases as conidial copulation. In the large majority of the previously investigated forms, it is replaced by true deuterogamous compensation.

Ascobolus citrinus will serve as an example of the parthenogamous group (Schweizer, 1923). At germination the ascospores swell, rupture the exospore and form one, rarely several germ tubes. After four to five days, especially in cultures rich in protein, there appear on branches of the hyphae, large clavate protrusions which are abjointed from the main hypha and subsequently develop to bow-shaped, slightly helical ascogonia (Fig. 227, 1 and 2). Besides the stipe cells, these contain usually six multinucleate cells of which the highest is distinguished by size and density of protoplasm. From the stipe cells, several thick hyphae which surround the ascogonium intertwine to a plectenchymatic

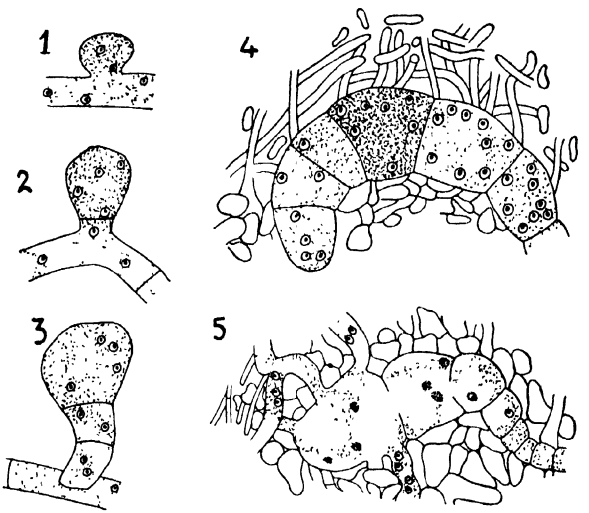


FIG. 227.—*Ascobolus citrinus*. Development of sexual organs. (× 725; *after Schweizer*, 1923.)

sheath and supporting tissue. In this condition, the fructification is about a quarter of a millimeter in size.

Through pores, the cells of the ascogonium come into open communication so that the nuclei of the other ascogonial cells migrate toward the large central cell. There they pair and pass out into the ascogenous hyphae, which radiate from this central cell only (Fig. 227, 5). The nuclei remaining behind degenerate. In contrast to *Pyronema confluens*, therefore, the sexuality of *Ascobolus citrinus* has been shifted toward the simpler Hypocreales, like that of *Polystigma rubrum*. Instead of amphimictic fertilization, there occurs parthenogamy, a cell fusion with the female organ.

A. stercorarius (Welsford, 1907), *A. glaber* (Dangeard, 1907), *A. immersus* (Ramlow, 1915), *A. Winteri* (B. O. Dodge, 1912), *Ascophanus carneus* (Cutting, 1909; Ramlow, 1915) correspond essentially with this

parthenogamous scheme. In *Ascobolus glaber*, the transition of the ascogonium to the main hypha is very gradual. Perhaps this degeneration in morphological differentiation is related to the degeneration of function. Conversely, the archicarp coils more than in *A. citrinus*, so that it forms a helix of two or three turns; when mature it consists of a two- to three-celled stipe, a two- to three-celled ascogonium, and at most a three- to four-celled trichogyne. In *Ascophanus carneus*, it is more strongly developed and consists of a three- to twelve-celled stipe, a three- to seven-celled ascogonium and a three- to five-celled trichogyne. Occasionally the latter is absent. Differing from *A. citrinus*, the nuclei do not migrate toward a single central cell, but the pairing is divided between two to three cells which usually lie near the top; consequently ascogenous hyphae develop from more than one ascogonial cell.

Similar differences in the number of privileged sexual cells appear in a third autogamous group. In *Ascophanus ochraceus*, *Saccobolus violascens* (Dangeard, 1907), *Thelebolus stercoreus* (Ramlow, 1906, 1915) and *Lasiobolus pulcherrimus* (Delitsch, 1926), the nuclear pairing takes place (*mutatis mutandis*) as in *Ascobolus citrinus*, in only one cell of the ascogonium; in others *e.g.*, *Rhyparobius* (*Thecoteus*) *Pelletieri* (Barker, 1904; Overton, 1906), as in *Ascophanus carneus*, several of them are shared in the formation of ascogenous hyphae.

In the form of its archicarp *Ascophanus ochraceus* connects directly to *Pyronema confluens*. On a single hypha (or on a few of them), there arises a small group of up to 15 stipitate, swollen unicellular ascogonia, each of which is provided with an occasionally branched trichogyne. Antheridia are no longer formed, the female nuclei pair, as occasionally in *Pyronema confluens*, within one ascogonial cell and migrate into the ascogenous hyphae.

Saccobolus violascens and *Rhyparobius Pelletieri* represent the type of multicellular ascogonium which we have come to know as the rule in the Ascobolaceae. In the former, however, nuclear pairing takes place in a single cell which alone functions as a mother cell of the ascogenous hyphae. In the latter, pairing may occur in any cell of the ascogonium, and the ascogenous hyphae develop from several cells of the ascogonium.

Thelobolus stercoreus, finally, forms an isolated, peculiarly reduced type which at present cannot be satisfactorily interpreted. The mycelium consists of uninucleate cells; out of one of these grows the ascogonium in a thick uninucleate branch. Later it becomes bi- to quadri- to octonucleate and then separates into several uni- and one binucleate cell. Ascogenous hyphae are not formed, but both nuclei of the single binucleate ascogonial cell fuse in the mother cell and go through several mitoses (up to ten), whereby the number of nuclei mounts to over 1,000. Meanwhile this fertile ascogonial cell has developed to a thick-walled ascus, which at maturity contains over 1,000 ascospores, and whose top shows

a definite dehiscence zone (Fig. 228). During this development, the ascogonium has been surrounded by sheath hyphae which, as no true apothecium is formed, surround the apothecium like a peridium. The unique character of *Thelobolus stercoreus* consists in that no ascogenous hyphae are formed, but one cell of the female apparatus develops directly to a single ascus. Perhaps *T. stercoreus* represents a degeneration series like that of the Erysiphaceae in the Perisporiales. In this case, *Thelobolus stercoreus* would correspond approximately to *Sphaerotheca Humuli.*

Pezizaceae.—As we remarked in passing, the same degeneration takes place in the Pezizaceae which we have followed in the Ascobolaceae. As *Lasiobolus brachyascus* in the Ascobolaceae is directly connected to *Pyronema confluens*, so two forms of the Pezizaceae studied so far are in close accord with this type, *Lachnea stercorea* and *L. scutellata.*

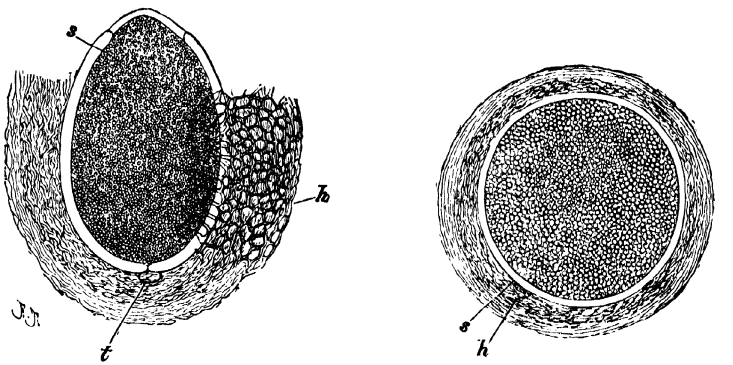


FIG. 228.—*Thelebolus stercoreus.* 1. Fructification in longitudinal section. The sheath, *h*, is only partially shown; actually, it entirely surrounds the ascus, *s*; *t* is the remnant of the ascogonium. 2. Mature fructification seen from above. (× 240; *after Brefeld.*)

Lachnea stercorea (Fraser, 1907; Fraser and Brooks, 1909) forms its small, densely tomentose, orange fructifications, about 4 mm. in diameter, on excrement of various animals, especially of cattle, during the winter and spring. On any hypha a pyriform ascogonium with a long trichogyne develops as a branch which is separated from the main hypha by several stipe cells. The trichogyne is not unicellular, as in *Pyronema confluens*, but is divided into 4 to 6 cells of which the terminal is the longest. An antheridium, as in *P. confluens*, comes into open communication with the trichogyne. In no case could a dissolution of the wall of the basal trichogyne cell and migration of the male nucleus be proved. Probably, as in certain nutritive conditions in *P. confluens*, the male nuclei degenerate in the trichogyne, whereupon the ascogonial nuclei, after a single division, pair autogamously and form ascogenous hyphae. Thus the antheridium as well as the trichogyne is only vestigial.

In *Lachnea scutellata*, which forms shining red fructifications on dead wood, generally no antheridium is formed and the ascogonia develop at once with autogamous pairing of their nuclei (Brown, 1911).

While in both these cases have been observed types of sexual activity such as can be produced experimentally in *Pyronema confluens*, three other Pezizaceae, *Lachnea abundans*, *Humaria granulata* and *H. rutilans*, have relationships which extend beyond *Pyronema confluens*.

Lachnea abundans connects directly to the parthenogamous Ascobolaceae (*Ascobolus citrinus* type). Its archicarp consists of a long, eight- to nine-celled trichogyne, transitorily projecting beyond the hyphal tangle, a three- to four-celled, helical ascogonium and a multicellular stipe. Antheridia have not been observed (Fraser, 1913). In the septa of the trichogyne, nevertheless, transitory pores are formed, possibly as atavism; since there are no foreign nuclei to pass through, however, the pores are again closed by callus plugs. Subsequently the septa in the ascogonium between three to four cells dissolve, nuclear pairing begins and the ascogonium develops, according to the known scheme, to ascogenous hyphae.

In the second group, *Humaria granulata* (Blackman and Fraser, 1906; Fraser and Brooks, 1909) and *H. anceps* var. *aurantiaca* (Delitsch 1926), the lack of antheridium has progressed so far morphologically that the ascogonium no longer forms a trichogyne. In contrast to *Lachnea abundans*, the ascogonium is unicellular, as in *Pyronema confluens* and the two first species of *Lachnea*. It has no trichogyne and hence appears externally like the oogonium of the Oomycetes (Fig. 229, *A*). Apparently without external cause, the nuclei pair and migrate into the ascogenous hyphae (Fig. 229, *C*). Here also we have autogamy; because of lack of antheridium, however, there is no trichogyne.

In *Humaria rutilans* even the ascogonia, which because of autogamy would be only a detour, are no longer formed and the sexual act takes place between any two vegetative cells in the hypothecium (Fraser, 1907, 1908). Autogamy in the interior of special branches of vegetative hyphae differentiated as sexual organs has been replaced by ordinary pseudogamy between the hyphae themselves. With these forms, the sexual processes of the Ascomycetes have reached a stage of degeneration which we shall observe later in various modifications under the Basidiomycetes.

Cytological investigations of a larger number of Pezizaceae will broaden and deepen the problems indicated here. Thus *Otidea aurantia* (Fraser and Welsford, 1908), *Humaria theleboloides* (*Peziza theleboloides*), *Humaria Roumegueri* and *H. carbonigena* (Gwynne-Vaughan, 1922) seem to possess a well-developed uni- or multicellular ascogonial region, while *Pustularia vesiculosa* (*Peziza vesiculosa*) (Fraser and Welsford, 1908) *Aleuria P. tectorial* (*tectoria*) (Gwynne-Vaughan, 1922) and *Plicaria Adae* (*Peziza*

domiciliana (Schultz, 1927) complete their development without a trace of female sexual organs. Until detailed investigations of these species are at hand it will be impossible to interpret them.

In any case, it is characteristic for the Ascobolaceae–Pezizaceae group that in both families there appears a degeneration of sexuality which runs parallel and in the same direction. In contrast to this parallelism in degeneration of sexuality, they are entirely distinct in morphology of their fructification.

Fundamentally they differ only in the behavior of their asci, which in the Ascobolaceae project above the hymenium at maturity, while in the

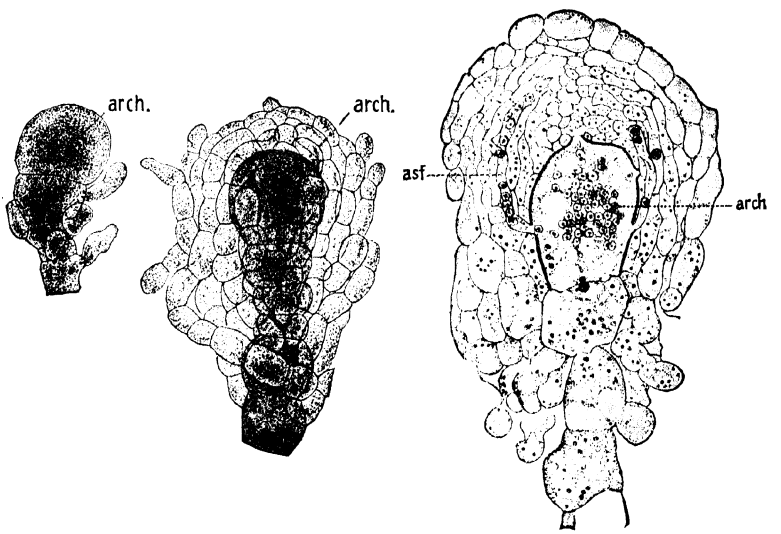


FIG. 229.—*Humaria granulata*. Development of the fructification. 1. Ascogonium, *arch*. 2. The same surrounded by sheath hyphae. 3. Autogamous nuclear pairing in the upper cell of ascogonium, *asf*. (1, 3 × 415; 2 × 285; *after Blackman and Fraser*, 1906.)

Pezizaceae, they retain their position between the paraphyses. The Ascobolaceae, however, in the outward form of the fructification, have remained very monotonous and have developed very little beyond the disc form, while the Pezizaceae have attained a higher anatomical differentiation and form latex vessels which secrete a colorless or white solution, which in *Plicaria succosa* turns yellow in the air, in *P. saniosa* blue. They also undergo distinct morphological development to stipitate, epigaeous cups, or to sphaerical, hypogaeous masses.

The simpler genera, as *Lachnea* and *Humaria*, may be placed close to the Ascobolaceae; they form flat, patelliform fructifications whose periphery is crenate or torn. In the epigaeous series, however, as *Pustularia*, *Discina* and *Acetabula*, a stipe becomes more and more

markedly differentiated (Fig. 230), and raises the fruiting disc over the substrate and finally, in *Macropodia* of the Helvellaceae, reaches a height of 2 cm. We will follow this line of development further.

In the hypogaeous series, on the other hand, the habitat of fructifications affects their morphological form. The fructifications of many Pezizaceae occur mainly on the earth from which they break forth at maturity. If one now imagines a fructification of this type always covered by the earth, so that the periphery arches over to a hollow sphere, one will have an idea of the structure such as is given for *Genea* (Fig. 242, 4) in the following order; a hollow, partially folded knob which is covered outside by a verrucose or short, tomentose rind and inside by continuous hymenium.

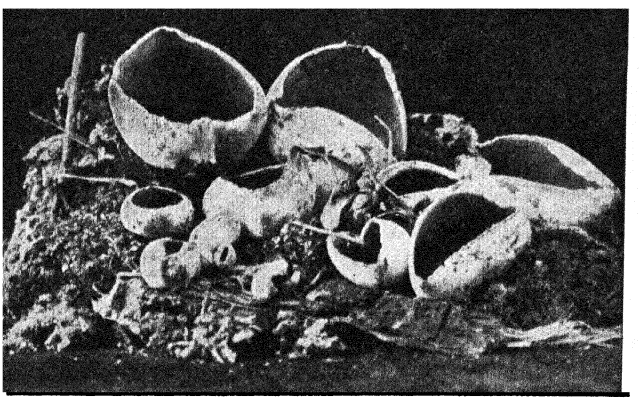


FIG. 230.—*Aleuria sylvestris*. Young and mature fructifications. (*After Seaver*, 1915.)

If one now imagines that the hymenium undergoes a marked lateral expansion and hence arches into the cavity of the sphere in folds and pads, one has a further developmental stage, to which *Sarcosphæra* (*Sepultaria*) belongs. In case the fructifications of this genus are formed directly under the surface of the soil so that they can break through, their tops may open lobately. If the layer of earth is too thick, they remain closed except for a small invisible opening, and then externally resemble truffles.

Finally, if one imagines these archings of the hymenophore so developed that at maturity the folds and indentations fill the whole cavity of the fructifications, we have *Geopora*, which belongs with the Tuberales as well as the Pezizales. Hence we will return again to this hypogaeous series in the Tuberales (E. Fischer, 1898, 1908; Gilkey, 1916).

Helvellaceae.—The last family of the Pezizales to be here discussed connects directly to the stipitate Pezizaceae, in *Macropodia*. By a

marked surface growth of their hymenia, they develop to very bizarre forms. As far as known, their fructifications develop hemiangiocarpously. Thus in youth the fructifications of *Hellvela elastica* form small, thick, hyphal tangles which gradually differentiate into stipe and pileus (McCubbin, 1910). At first one of these tangles is entirely surrounded by a sheath or a veil; later this is torn and the hyphae arrange themselves on the upper side of the pileus in a palisade, the future hymenium. First this palisade is concave, then it expands laterally, bends up to the shape of a saddle, and finally hangs down on both sides in two equal lobes; between these two lobes of the hymenium project two flaps forming a structure similar to that in Fig. 231, right; only in *H. elastica* are the two lobes often unequally developed, one being often more distended

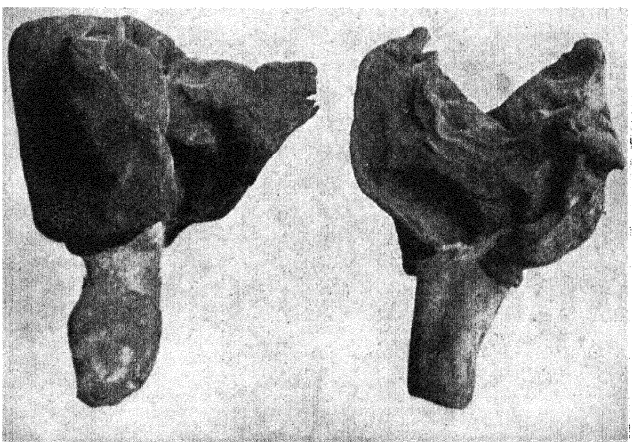


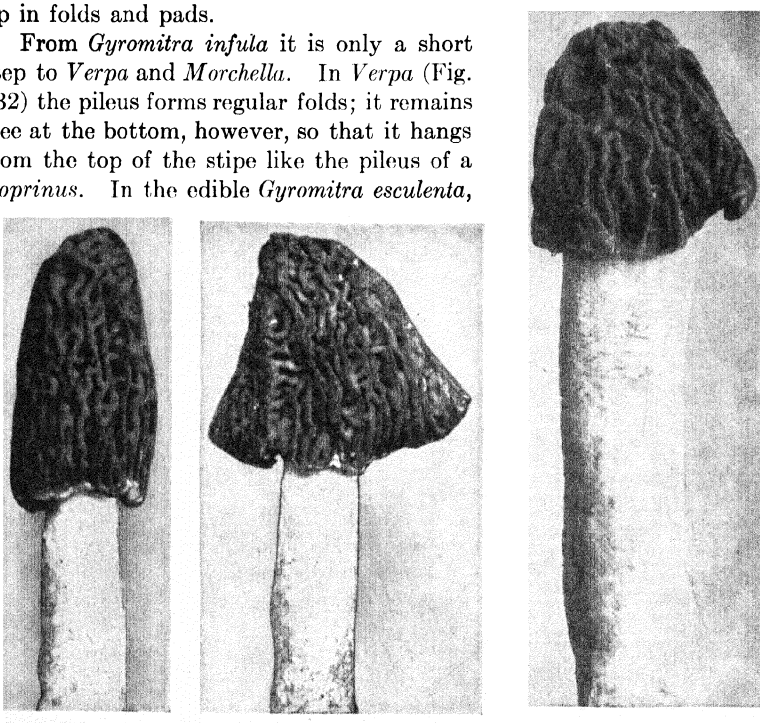
FIG. 231.—*Gyromitra infula.* (*After Falck*, 1916.)

than the other. As in *Humaria rutilans*, the ascogenous hyphae arise from ordinary vegetative hyphae of the hypothecium. In *Helvella crispa*, pseudogamous copulations occur between these hyphae (Carruthers, 1911). When the hooked tips of the ascogenous hyphae come into open communication with the main hypha, the nucleus migrates back into the hypha, forming structures similar to the clamp connections of the Basidiomycetes.

The fructifications of the other species of *Helvella* at first resemble those of *H. elastica;* even in *H. ephippium* the pileus is patelliform and concave in youth; later it becomes saddle-shaped and finally bends down in two lobes. In this species, the tips of both saddle wings are drawn out to very sharp points projecting above the fructifications. In *H. lacunosa* the fruit disc is, on account of the marked surface expansion, thinner, more fragile and more variable. In order to furnish support so that it

will not be destroyed before spore formation, the periphery of the pileus grows into the stipe below. *Gyromitra infula* belongs to this type (Fig. 231). The pileus lobes have coalesced and grown to the stipe, forming a hollow, campanulate structure with the hymenium outside. The surface growth of the hymenium continues even after this coalescence; being fixed below, however, the hymenium can no longer follow it and arches up in folds and pads.

From *Gyromitra infula* it is only a short step to *Verpa* and *Morchella*. In *Verpa* (Fig. 232) the pileus forms regular folds; it remains free at the bottom, however, so that it hangs from the top of the stipe like the pileus of a *Coprinus*. In the edible *Gyromitra esculenta*,



a *b* *c*

FIG. 232.—*Verpa bohemica*. *a*, *b*. Immature fructifications; *c*. Mature fructification. (*After Falck*, 1916.)

it is still free and entirely smooth in the young specimens just emerging from the soil; later, as in *H. lacunosa*, it coalesces with the stipe and then lies in deep, tortuous, forking and intersecting folds.

In the highest forms of the family, the morels, these folds are still more marked, they gradually become arranged with their interiors together and develop to knife-like ridges and groinings. The backs of these groins are sterile, so that the fertile layers are divided into numerous lacunose hymenia. In the simplest species, as *Morchella rimosipes* (Fig. 233), the lattices run chiefly meridionally and are comparatively little indented. In the higher forms, as *Morchella esculenta*, the hymenial

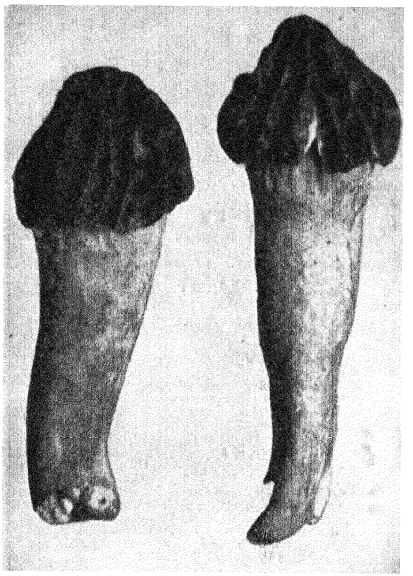
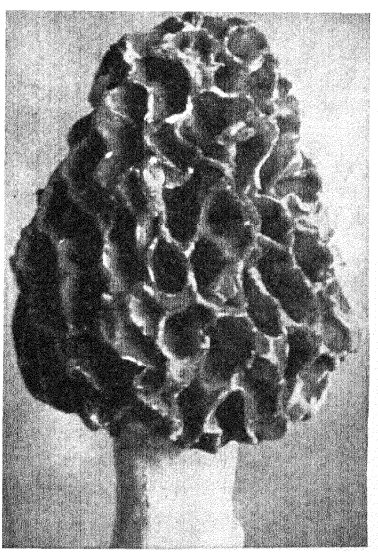


FIG. 233.—*Morchella rimosipes*. Mature fructification. (*After Falck*, 1916.)



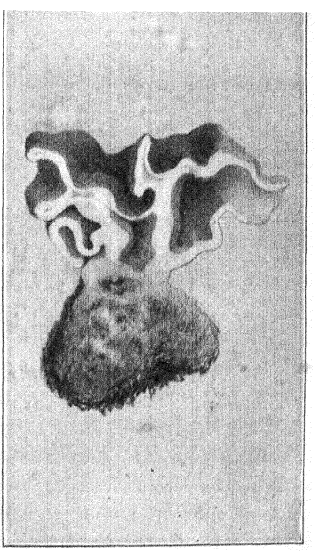


FIG. 234.—1. *Morchella esculenta*, surface view of fructification. (*After Falck*, 1916.) 2. *Gyromitra curtipes*, section showing chambers resulting from branching of chamber walls.

chambers extend into the fructification (Fig. 234, *b*) and are nearly enclosed. Even in these highest forms, the meridianal folds are bound by transverse ones in a regular network which morphologically is equal to that of the higher Gasteromycetes. As *Morchella esculenta* can discharge its ascospores to a height of several centimeters, one might conclude that the hymenia in the deeper chambers would shoot against each other; it seems, however, that the difference in temperature and dampness between the interior of the chambers and the outer world causes currents of air which bear the spores outward (Falck, 1916).

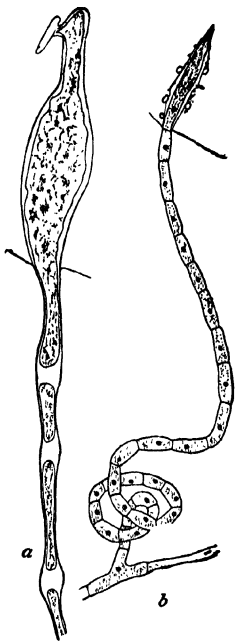


FIG. 235.—*Collema crispum*. Development of sexual organs. *a*, trichogyne which has copulated with a "conidium," the septa have already dissolved. *b*, ascogonium with trichogyne, several conidia clinging to the free end of the latter. (*After Baur*, 1898.)

Discomycetous Lichens.—Herewith we have ended the discussion of the Pezizales. As numerous representatives of this order have united with algae to form lichens and as these Discomycetous lichens play an important part in the derivation of the Ascomycetes from the Florideae, we will add a short discussion of the sexual relations of this group. We will limit ourselves here expressly to the ontogeny of the more important types and for all the remaining questions refer to the works of A. L. Smith (1921) and Tobler (1925). The previously investigated Discomycetous lichens have in common with the higher Pezizales, first, that their carpogonia do not proceed directly from the vegetative hyphae of the hypothecium but from deeply staining primordial hyphae, the so-called generative hyphae. Further, a large number of their genera (Saettler, 1914, mentions 24), like many Pezizales, possess helical or tangled ascogonia with trichogynes which transitorily project into the open. In the Discomycetous lichens, however, antheridia similar to those of the Pezizales are unknown. As far as there is a sexual act, it must occur according to the *Ascobolus carbonarius* type or be replaced by deuterogamy.

The fact that numerous lichens possess pycnia and that their trichogynes occasionally secrete a slimy substance by means of which they can hold fast the pycniospores (spermatia) brought by the rain, suggests the *Ascobolus carbonarius* type. Actually one sees conidia (spermatia) clinging fast to the trichogynes, and in *Collema crispum* it has been demonstrated that between the trichogyne tip and the conidium appears an open communication whereupon the septa of the trichogyne disappear (Fig. 235). This allows one to conclude that the conidial nucleus

migrates to the ascogonium, which subsequently develops ascogenous hyphae (Baur, 1898).

In *Collema pulposum* or a closely related species, a different behavior has been determined. Here the conidia, as in *Ascobolus carbonarius*, do not fall away but remain on the conidiophores. Hence the trichogyne grows, as in *Ascobolus carbonarius*, over the thallus surface toward the conidiophores and unites with them (Fig. 236). In these lichens the more migration of the conidial nucleus into the trichogyne has been demonstrated; the nuclear relationships in the ascogonium are so complicated,

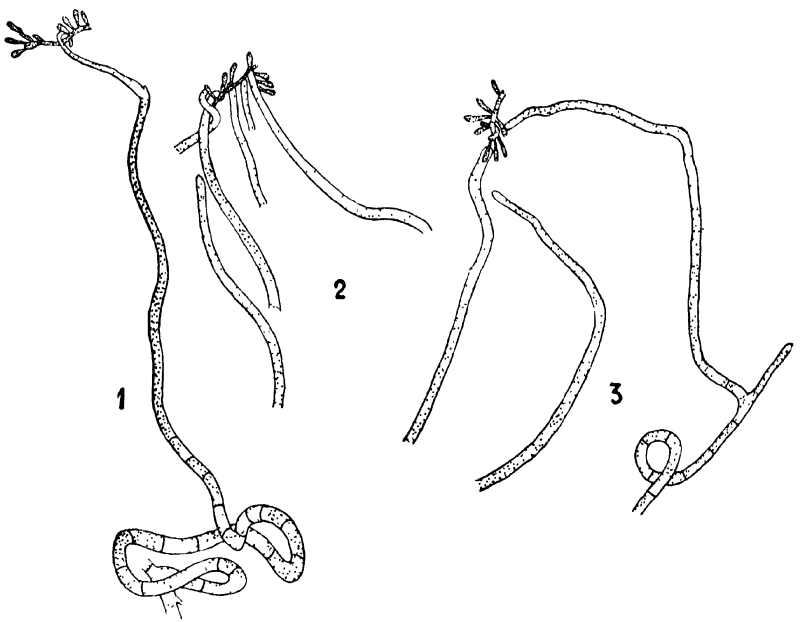


FIG. 236.—*Collema pulposum*. Trichogyne growing toward conidiophore. (× 345; *after Bachman*, 1912.)

however, that their further fate cannot be followed (Bachman, 1912, 1913).

Because of this property of copulation with trichogynes, the conidia of lichens have been considered specialized male sexual cells and called spermatia and the pycnia correspondingly have been called spermagonia. Moeller (1887, 1888) and Istvanffi (1895) working with impure cultures have denied the assumption of this specialization, as the pycnidiospores may develop in culture to mycelia, as normal imperfect forms. More probable is the interpretation which already has been brought forth in connection with *Ascobolus carbonarius;* that it is a question of ordinary

imperfect forms which, when the male sexual organs are lacking, can function subsidiarily with the pseudogamous fertilization of the trichogyne. The strongest support for this conception would be found if the trichogynes could copulate with ordinary vegetative hyphae. No such case, however, has yet been observed. Just as in the Pezizales, so in the Lichens, this amphimictic sexuality of the *Ascobolus carbonarius* type is still further withdrawn and replaced by deuterogamy. It appears first that copulation with conidia is no longer complete. Thus, in *Anaptychia ciliaris* (Baur, 1904) and possibly also in *Physcia pulverulenta* (Darbishire, 1900) there still appears an open communication between conidium (spermatium) and trichogyne tip but no nuclear migration occurs and the trichogyne walls are no longer dissolved; instead there occurs, at least in the former, a parthenogamy between ascogonial cells, upon which the ascogenous hyphae develop. As in *Lachnea stercorea* and, under certain conditions of nourishment, in *Pyronema confluens*, the amphimictic sexual act is introduced but no longer completed and replaced by deuterogamy.

As a consequence of this emancipation of conidial fertilization, it is well to observe, as in *Cudonia lutea* of the Geoglossaceae, the trichogynes projecting into the open are formed in species which lack conidia. Whether the trichogynes here are of a rudimentary character and regarded more ontogenetically, will soon disappear or whether they are conserved by a change in function, is at present still uncertain. Lindau (1899) imagined that the trichogynes, which are functionless as sexual organs, assist in the opening of the thallus for the hymenia and in the taking up of oxygen and hence he calls them terebrator hyphae; his interpretation, however, rests upon histologically incorrect conceptions.

As in the Pezizales, the functionless trichogynes of the Discomycetous lichens rapidly degenerate. At first in *Parmelia acetabulum* (Moreau, 1922) and *Icmadophila ericetorum* (*I. aeruginosa*) (Nienburg, 1908), as in *Cudonia lutea* of the Pezizales, they undergo an early degeneration and the sexual acts are then apparently parthenogamous or pseudogamous.

As in the Pezizales, this functional degeneration then becomes morphological. Thus in *Cladonia gracilis* (Wolff, 1905), as in *Rhizina undulata* of the Pezizales, the typical helical form is lost and the ascogonia form only thick, deeply staining, irregularly twisted hyphae.

In *Parmelia tiliacea* (Lindau, 1888), *Xanthoria parietina* (Wolff, 1905) and *Baeomyces rufus* (*Sphyridium byssoides*) (Nienburg, 1908), as in *Spathularia velutipes* and *Humaria granulata* of the Pezizales, trichogynes are no longer formed, thus still more effacing the specific character of the ascogonia.

Finally, as in *Baeomyces roseus* (Nienburg, 1908), *Stereocaulon paschale* (Wolff, 1905) and *Solorina saccata* (Moreau, 1916), like *Trichoglossum hirsutum*, *Humaria rutilans*, *Pustularia vesiculosa* and *Aleuria tectoria*

of the Pezizales, ascogonia are no longer formed and the ascogenous hyphae develop directly from the generative or vegetative hyphae.

In the lichens pure amphimictic forms (of the *Ascobolus magnificus* type) are still unknown, but our acquaintance begins with the first stage of degeneration of the *Ascobolus carbonarius* type. It may be again emphasized here, however, that these relationships are generally otherwise interpreted, namely, as in favor of a derivation from the Florideae. As we shall again meet similar phenomena in the Laboulbeniales, the discussion of the various theories of derivation of the Ascomycetes will be deferred to the review at the close of the Laboulbeniales. The Pezizales here show a very heterogeneous arrangement which begins with the lower forms rooting in the Plectascales and Myriangiales and rises above the Polyporaceous type to highly differentiated agaricaceous forms. The sexual organs connect directly to the antheridia and ascogonia of the Gymnoascaceae and Aspergillaceae and proceed to a further morphological development. Then the antheridia degenerate and the original gametangial copulation is replaced by deuterogamy, first by parthenogamy, then by autogamy and finally, after the ascogonia have disappeared, by pseudogamy. With this degeneration of sexuality the ascogenous hyphae gradually lose their special character and change their form by fusion of the hook tip with the stipe cell and a further outgrowth of the hook to a clamp mycelium which penetrates the fructifications for long distances.

CHAPTER XXIII

TUBERALES

In the Tuberales we meet for the third time a hypogaeous developmental series. The first group we met in the Endogonaceae among the Zygomycetes; the second in the Terfeziaceae and Elphomycetaceae of the Plectascales; the third group is related directly to the Pezizales in the Discomycetes.

In many cases the mycelium surrounds the roots of forest trees and forms mycorrhizas. Their fructifications are connected with this mycelium over their whole surface or only at their base. Because of their hypogaeous growth, the young stages of these fructifications are little known. In *Tuber*, the ascogenous hyphae, as in *Leotia lubrica* of the Geoglossaceae, are present even in the earliest stages and have kept pace with the expansion of the fructification (Bucholtz, 1897). The asci of *Tuber brumale* var. *melanosporum* (Dangeard, 1894), *T. dryophilum* and *Hydnobolites* (Faull, 1905) arise according to the hook type while those of *T. aestivum* (Schussnig, 1921), are intercalary, as in the lower Plectascales.

Similarly, the systematic position of many genera is still uncertain, since only a knowledge of the youngest stages is needed for an interpretation of the mature fructifications. At present, within the order two series, the *Hydnotrya–Tuber* and the *Genea–Genabea* series, may be distinguished.

Hydnotrya of the first series connects directly to the *Sphaerosoma* and *Mycogalopsis* of the Pezizales. In some species of *Sphaerosoma*, the fructifications show a semihypogaeous, tuberous, hollow sphere whose whole exterior is covered by hymenium; the surface of this hollow sphere is divided by irregular folds into flat warts and grooves. *Hydnotrya* is thus a *Sphaerosoma* in which the folds have penetrated still deeper into the fructification, and become passages or canals (Fig. 237, 1). The formation of the asci is limited to the walls of these passages, while on the exterior the walls of the hyphal palisade remain sterile and change to a brown rind. Thus, in a cross section through a *Hydnotrya* fructification one finds outside a thin rind layer of brown swollen hyphal tips which at the entrance of the cavities continue into the paraphyseal palisade. In the interior of the fructification, there is a confused system of canals or passages which generally open outwards at many points, more rarely converge to a single point; their wall is covered by a true hymenium composed of paraphyses and asci. The asci generally form a layer, as in the

true Discomycetes; some of them, however, apparently from lack of room, lie crosswise in the subhymenium.

In *Balsamia* the characters just sketched for *Hydnotrya* are still more marked. The verrucose rind usually consists of pseudoparenchyma. The palisade arrangement disappears and the clavate asci become ellipsoidal or spherical as space permits. In *Pseudobalsamia* the cavities still open outward, as in *Hydnotrya*. In the Californian *Pseudobalsamia magnata* (*P. Setchelli*) the majority of the cavities run toward a pitted

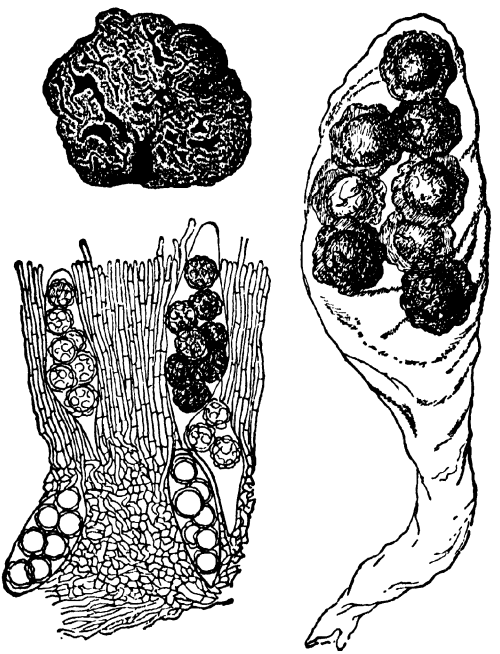


FIG. 237.—*Hydnotrya Tulasnei*. 1. Longitudinal section of mature fructification. 2. Section of portion of hymenium. 3. Ascus. (1 × 8/5; *after Tulasne and E. Fischer.*)

depression in the top of the fructification (Fig. 238). In *Balsamia, sensu strictiore*, the openings generally disappear so that after a certain time the chambers form true cavities (E. Fischer, 1908; Bucholtz, 1910). In certain forms, as *P. magnata* (Fig. 238), we meet another peculiarity which will play a decisive role in the further form of the *Hydnotrya–Tuber* series; in these forms, the paraphyses (as in the epithecial formation of many Pezizales) continue their growth out over the hymenium and intertwine over the top of the asci with the paraphyses of the opposite side, forming a loose tissue which fills the cavities for a long distance (indicated in Fig. 238 by a light stippling).

In the cavities of *Pachyphloeus*, this secondary tissue has developed to a pseudoparenchyma of looser structure than the ground tissue. In a cross section through a mature fructification it appears penetrated by two sorts of veins (Fig. 239, 1 and 2). One, the so-called tramal plates (generally darker) or **venae internae,** which arising in the tissue zone lying under the rind, converge toward the top and bear the hymenial palisade on their surface, and the other, **venae externae** (generally lighter), which begin at the top of the fructification, penetrate its interior and end blindly. Between the two systems of veins there lies a hymenium consisting of parallel paraphyses and asci arranged in a regular palisade with tips directed toward the venae externae. Ontogenetically the venae internae are only the folded parts of the wall of the hollow sphere of the fructification, such as we have come to know in *Hydnotrya*, while the venae externae form the originally looser, later pseudoparenchymatous tissue which

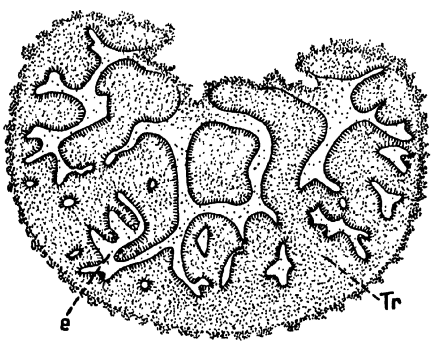


FIG. 238.—*Pseudobalsamia magnata.* Median section of fructification. (× 6; *after E. Fischer*, 1908.)

has arisen by the growth of the paraphyses and secondarily has filled the hollow passages in the interior of the fructification. By these venae externae the fructifications of *Pachyphloeus*, in contrast to those of *Hydnotrya*, form a compact mass, though ontogenetically heterogeneous, such as we usually meet in *Tuber*.

Apparently in *Tuber*, the fructifications, as in *Hydnotrya* and possibly in the above genera, are formed gymnocarpously (Bucholtz, 1897, 1903). Thus, Fig. 239, 3 shows the stage of 1.5 mm. cross section; a flat shell on whose interior project several tramal plates, venae internae. This flat shell is sometimes called ground plate. Apparently it corresponds to the hypothecium of apothecia but is histologically more differentiated and is penetrated by special wide-lumened hyphal strands of unknown function, frequently called resin canals. Outside, the ground plate is surrounded by a brown pseudoparenchymatous ground tissue, the peridium, which, extending beyond the rind, gradually merges with the pali-

sade tissue. Then follows the ground tissue from which the tramal veins branch. In the course of development, the whole cavity is surrounded by the ground plates and gradually filled by the tramal pads; as these are much twisted and bent, sections of the interior of the fructification show isolated cavities which probably were exposed originally.

In the mature fructification (Fig. 240, 1), as in *Pachyphloeus*, one finds without a verrucose rind 1 mm. thick and within a dark-colored flesh, penetrated by both labyrinthiform systems of slender veins; the original

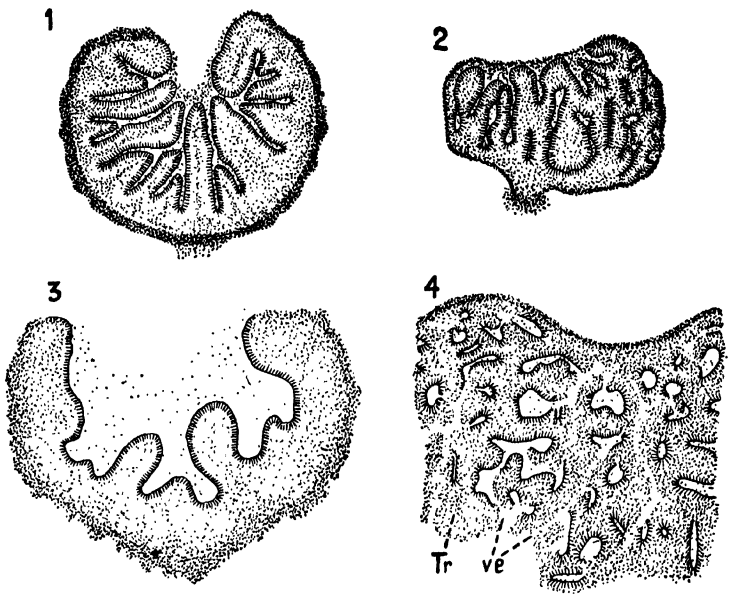


FIG. 239.—1. *Pachyphloeus melanoxanthus*. Section of mature fructification. 2. *Pachyphloeus luteus*. Section of fructification. 3. *Tuber excavatum*. Section of young fructification, cavity beginning to fill with loose hyphal tissue. 4. *Piersonia bispora*. Peripheral portion of immature fructification. *tr*, tramal plates; *ve*, venae externae. (3 × 26; 4 × 6; *after E. Fischer*, 1897, 1908; *Bucholtz*, 1897.)

white or reddish venae externae, ochraceous at maturity, and the dark-brown venae internae, often almost obliterated at maturity. In the subgenus *Aschion* the venae externae converge toward a point, while in the subgenus *EuTuber* they radiate toward certain points of the periphery and open outward; in some species this opening is not visible as the venae externae are enclosed at the periphery by a compact hyphal tissue.

The regular structure of the hymenium which was gradually disappearing in *Hydnotrya* and *Pachyphloeus*, is entirely lost in *Tuber* (Fig. 240, 2). The asci (ellipsoid or pyriform) lie irregularly imbedded in a tissue between the venae. The spore number has become inconstant

and may sink from eight to four to two to one, with proportional increases in size. The spores generally become multinucleate while still inside the ascus. The entire morphological and biological development of the asci which we could follow from the Plectascales to Pezizales, their biological discharge apparatus, their transition from spherical to clavate

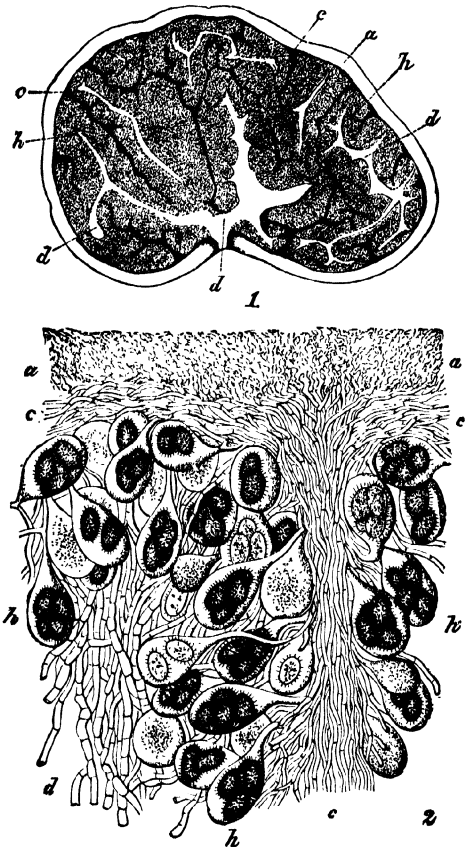


FIG. 240.—*Tuber rufum*. 1. Section of fructification. 2. Portion of interior of fructification. *a*, rind; *c*, venae internae (trama plates); *d*, venae externae; *h*, hymenium. (*After Tulasne.*)

form and their arrangement in regular hymenia, has degenerated in the Tuberales on account of their endogenous formation; they have lost their function of spore dissemination, apparently also their clavate form and arrangement in hymenia. The striking correspondence between *Tuber* and the Plectascales is, according to this concept, only a convergence phenomenon.

Various species of *Tuber* are used as food.

While *Tuber* continues the *Hydnotrya–Pachyphloeus* series in a vertical direction, a side line, the *Piersonia–Choiromyces* series, undergoes a curious modification. In *Piersonia bispora* the hyphal palisade does not, as in the other Tuberales, form asci over the whole expanse of the passages, but only in the innermost blind branches (Fig. 240, 4) which then are widened into chambers (E. Fischer, 1908) and, in a certain sense, correspond to the gleba chambers of the Gasteromycetes. As an exception, asci may also occur in the sterile palisades, but they no longer mature. If one wishes to consider the *Sphaerosoma–Pachyphloeus* series as tending to remove the hymenium from the surface into the interior of the fructification and there to gradually adjust it to the whole tissue of the fructification, *Piersonia* forms a fundamental extension to this principle; the hymenia are moved still more toward the interior and have entirely lost

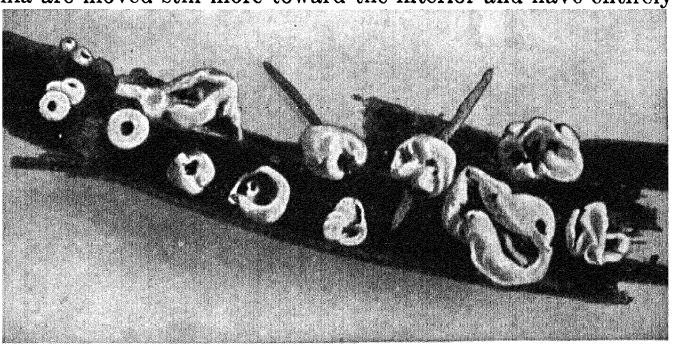


FIG. 241.—*Genea Thwaitesii*. Fructifications. ($\times \frac{2}{5}$; *after Petch*, 1907.)

contact with the exterior of the fructification. The step from *Sphaerosoma* to *Hydnotrya*, with limitation of the hymenium to the interior of the fructification, has been repeated from *Pachyphloeus* to *Piersonia;* here, however, the formation of asci is localized to the innermost endings of the passages within the fructification.

If one imagines the hymenial chambers of *Piersonia* better developed, so that in cross section the hymenia form long tortuous bands and if one imagines the venae externae obliterated, so that a functionless palisade grows in from both sides connecting the ground tissue of both sides, one has *Choiromyces* (Bucholtz, 1908) in which the mature hymenia lie in the interior of fleshy fructifications without suggestion of passages.

In the *Genea–Genabea* series, the fructifications of *Genea Thwaitesii* (E. Fischer, 1909), as possibly those of all Tuberales, begin as small hyphal tangles. Instead of the knot developing to a hollow sphere into which the tramal plates grow, in *Genea Thwaitesii* the hymenium arises

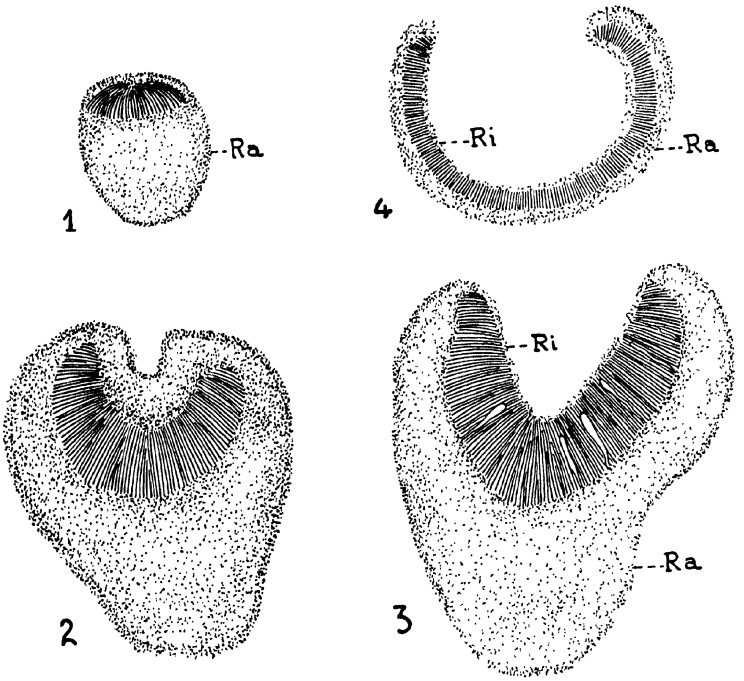


FIG. 242.—*Genea Thwaitesii*. Development of fructification. (1 to 3 × 100; 4 × 24; *after E. Fischer*, 1909.)

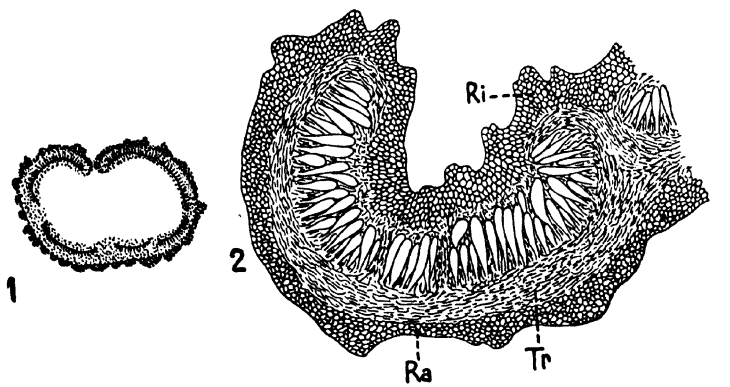


FIG. 243.—*Genea* (*Myrmecocystis*) *Vallisumbrosae*. 1. Section of fructification (× 6). *Genea* (*Myrmecocystis*) *cerebriformis*. 2. Section of hymenium (× 42). (*After Bucholtz* 1901; *E. Fischer*, 1908.)

endogenously. In the youngest known stage, measuring about ¼ mm. (Fig. 242, 1), as in many lichens, *e.g.*, *Physcia pulverulenta*, *Anaptychia ciliaris* and *Usnea barbata*, the hymenial palisade is formed angiocarpously at the tip of the fructification under the outer rind *Ra.* In course of further development, the margins bend over strongly so that the fertile layer becomes patelliform (Fig. 242, 2 and 3). Later, by a strong lateral growth, it gradually forms a comparatively smooth hollow sphere, in which the hymenium (Fig. 242, 4) is not free but covered by the rind *Ri* which consists of swollen and septate paraphyseal tips and corresponds apparently to the epithecium of the Pezizales.

From *Genea Thwaitesii*, the development may be followed in two directions. In *Genea* the same process which we have met in the development of ascocarps of *Tuber*, is repeated. In the subgenus *Heterogenea*, (*G.* (*Heterogenea*) *Gardneri* and *G.* (*Heterogenea*) *Harknessii*) numerous ingrowing projections of the cavity tend to separate the fertile areas, while the spores become less ellipsoid. In the subgenus *Myrmecocystis*,

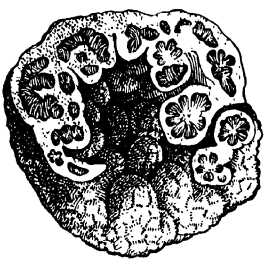


FIG. 244.—*Genabea fragilis.* (× 5; *after Tulasne.*)

however, the spores have become spherical and verrucose. If we only had the end members of the series we would probably regard them as separate genera, but the transition forms seem to indicate that they are better kept together.

Thus the hymenium is no longer laid down in a continuous layer, but separated into several parts by sterile ground tissue, as may be seen in Fig. 243, 1, in *G.* (*Myrmecocystis*) *Vallisumbrosae*, which consists of irregular, spherical, hollow fructifications, occasionally slightly plicate, about 1 cm. in diameter with one or two round fissures. Thus the subgenus *Myrmecocystis* differs from *Eugenea*, as *Piersonia* from *Pachyphloeus*, by the localization of the hymenium on limited areas. As in the *Sphaerosoma–Hydnotrya* series, here the wall of the fructification curved into the interior of its cavity with folds and projections and thereby, as in *G.* (*Myrmecocystis*) *cerebriformis* (*Pseudogenea californica*) became an entirely irregular, tortuous structure. The single hymenia are more or less bent, being concave toward the central cavity of the fructification; the ascus tips, therefore, lie toward the interior of the hymenophore on the

exterior of the hymenium. From the hymenophore, a bundle of paraphyses penetrates the hymenium and passes through it into the inner rind *Ri* (Fig. 243, 2). This is more strongly developed than in *Eugenea* and forms a pseudoparenchymatous rind, which is elevated in spots to pyramidal warts. *Delastria rosea*, formerly included in the Terfeziaceae, seems to show the highest development in this series.

If the cover layer *Ri* is further developed, so that the hymenium lies farther in the interior of the fructification, we have *Genabea*, shown somewhat schematically in Fig. 244. Because of the irregular course of the folds and canals, most of the hymenia are cut obliquely and hence appear irregularly arranged. In cross-section, however, they are crescent shaped with the concave side toward the hollow passages.

If we review the genera of the Tuberales here discussed, their relationships may be approximately given in the following scheme:

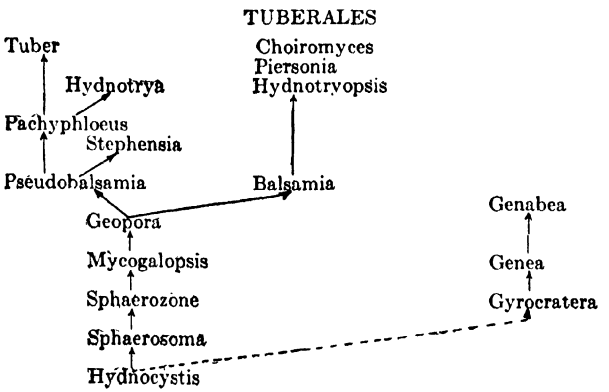


DIAGRAM XXIV.

Thus the Tuberales form two convergent series, the probably gymnocarpous *Sphaerosoma–Choiromyces* series and the hemiangiocarpous *Genea–Genabea* series. In the former, from the *Sphaerosoma*-like Rhizinaceae, the *Hydnotrya–Balsamea* group arises by a strong lateral development of the hymenium which causes a deepening of the folds and by a localization of the asci in the interior of the passages. The hollow passages are filled by a loose pseudoparenchyma arising from the paraphyseal layer, so that the structure of the fructifications becomes massive (*Pachyphloeus–Tuber* group). Subsequently the formation of hymenia is more and more limited to the last blind ends of passages (*Piersonia*) and finally these passages coalesce completely and the hymenia lie in closed chambers (*Choiromyces*).

The relationships of the *Genea–Genabea* series are not so simple. There is no doubt that in the formation of their fructifications, the same mor-

phogenetic forces (unequal growth of outer and inner fructification layers and consequent folding and curving of fructification wall, localization of formation of asci, etc.) have been active, as in the *Sphaerosoma–Choiromyces* series. The significance of the layer *Ri*, and consequently the whole position of the series, however, is still obscure. The development of *Genea Thwaitesii* leads one to suppose that the layer *Ri* is a true epithecium, that has developed after the fraying of the parts of the outer rind *Ra* lying above the fructification. In this sense, *Genea* might be connected to the hemiangiocarpous Pezizales, particularly to the Pezizaceae. After *Genea*, the epithecium has undergone a special development to a pseudoparenchymatous cover layer which possesses no analogue in the Discomycetes. Thus an explanation can only result from an ontogenetic investigation of the young stages.

CHAPTER XXIV

LABOULBENIALES

The Laboulbeniales form their fructifications only on the chitinous integument of living insects. When examined in situ they appear like minute, dark-colored or yellowish bristles or bushy hairs, usually scattered, but often densely crowded over certain areas on which they form a furry coating. Although they may be said to produce a contagious cutaneous disease, they give rise to no fatal epidemics, such as are sometimes associated with *Cordyceps* and *Entomophthora*. The very existence of these parasites seems to depend on the fact that the host is not destroyed, since their own life ends with that of the insect. The habit of growth is external, unassociated with extensive development of haustoria, except on certain groups of soft-bodied insects, where widely divergent groups have developed extensive rhizoidal processes of the basal cell, which penetrate the interior of the host.

Such an external parasitism on living and usually actively locomotive, often aquatic hosts, is associated with a comparatively simple structure adapted to the exigencies of such a life. A simple receptacle is fixed by means of a usually blackened base or foot, to the integument of the host. This receptacle gives rise to certain appendages, commonly connected with the production of the male sexual organs, while perithecia are usually produced from the same receptacle, except in certain dioecious groups.

Most species of Laboulbeniales are limited to definite genera of insects and in a few instances, *e.g.*, *Chitonomyces* on *Gyrinidae* and *Laccophili*, even to definite restricted areas of attachment in different host individuals of different species, from even different regions. For example, not only will the distance from the apex of the elytron of the area occupied by a given species always be about the same, but its relation to either margin will be more or less definitely fixed. Of species inhabiting the left elytron, none will be found even in a corresponding position on the right.

The Laboulbeniales may be divided into three families, distinguished by the relative development of the male sexual apparatus. In the more primitive Ceratomycetaceae, the antheridia are exogenous, bearing free spermatia on the specialized branches of appendages. In the Laboulbeniaceae, the spermatia are produced in unicellular, flask-shaped antheridia, while in the Peyritschiellaceae the antheridia are compound, discharging the spermatia into a common cavity, from which they are subsequently expelled.

Ceratomycetaceae.—This family of fifteen small genera on aquatic insects, Hydrophilidae, contains some of the most striking forms, yet little studied ontogenetically.

In *Ceratomyces mirabilis*, the young individual consists of a simple series of superposed cells, of which the distal begins to branch at an early age. One of the intercalary cells of this series divides longitudinally, the upper cell becoming a finger-like projection, the primordium of the perithecium. The primordium divides into three cells, the upper becoming the simple trichogyne, the middle the trichophoric cell and the basal, not projecting from the axis of the plant, becoming the carpogenic cell. The sister cell to the primordium divides into an outer and an axial cell. The lower cell has also divided longitudinally into two cells, one of which grows outward and upward, forming one row of the wall and canal cells of the mature perithecium. The axial cell apparently gives rise to the other three rows. These wall cells grow beyond and around the carpogenic and trichophoric cells and, by subsequent division, form the perithecium. The development of the perithecium will be described in greater detail in the Laboulbeniaceae (p. 369). The spermatia develop from the segmentation of slender branches into bacilliform bodies which fall from their attachment as soon as formed. *Rhynchophoromyces rostratus* (*Ceratomyces rostratus*) has the same general ontogeny (Fig. 253, 1) except that the whole base of the appendage becomes incorporated with the developing venter of the perithecium until it seems to arise from the wall cells. The neck in this species becomes abruptly reflexed at maturity.

In *Coreomyces* we have a new type of perithecial development. The young individual of *Coreomyces Corisae* consists of three cells, from the uppermost of which appendiculate cells are cut off distally. Above the appendiculate cells is a series of four to six superposed cells terminated by a sterile appendage. Thus there are three regions of which the two basal cells form the receptacle, the appendiculate cells the antheridia, while the distal region forms the perithecium. As the development proceeds, the sub-basal cell of the distal region proliferates into the cell above, while the sterile appendage above breaks off (Fig. 245, 3). The penetrating branches, usually two corresponding to the posterior basal cell and the secondary stalk cell of the ordinary perithecium (p. 370), continue to develop the perithecium. The developing perithecium destroys the septa of the cells above, sending the trichogyne through the septum at the base of the previous sterile appendage (Fig. 245, 4). At maturity, the vestigial wall cells of the perithecium degenerate, leaving the developing ascogonium surrounded only by the walls of the original cells of the distal region, a **pseudoperithecium** (Fig. 250, 2). Thus the asci and spores finally float free within a structure resembling a perithecium and performing the same function, but ontogenetically having little in common with a perithecium.

The antheridia are the lower cells of the appendage or its branches which function as discharge tubes through which the spermatia make their way. This character forms a transition to that of the Laboulbeniaceae (Fig. 250, 5).

The highest vegetative development in the order is found in *Zodiomyces* (Fig. 246). The spore (Fig. 247, 6) germinates by forming many

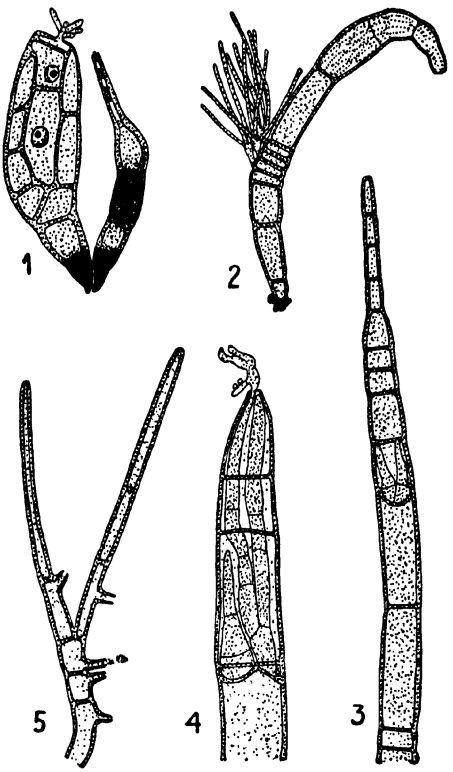


FIG. 245.—*Amorphomyces Falagriae*. 1. Male and female individual developed from same spore pair. *Coreomyces curvatus*. 2. Mature individual. 3. Upper portion of young individual beginning to form the archicarp in the upper cells. 4. Older individual, showing trichogyne. 5. Male appendage, showing spermatial formation. (1 × 880; 2 × 200; 3 × 410; 4, 5 × 705; *after Thaxter*, 1908.)

transverse divisions in both segments. The distal cell gives off a variable number of branches, the future primary appendage. Longitudinal division sets in until there is a massive clavate structure terminated by a tuft of the primary appendage (Fig. 247, 1 to 3). A more rapid growth at the base of this appendage causes the wall cells of the region to arch out forming a cavity within (Fig. 247, 4). As the cavity enlarges, secondary appendages begin to grow upward and inward from the inner surfaces

of its lateral walls. These rupture the outer wall at the base of the primary appendage. The cavity continues to grow until the perithecia form from the base of the circle of secondary appendages. The antheridial appendages (Fig. 247, 7) usually consist of three superposed short cells bearing at the tips one to three large, bacilliform spermatia, which soon fall off and are sought by the trichogynes. Although the perithecia arise endogenously, their development is normal (Fig. 247, 8).

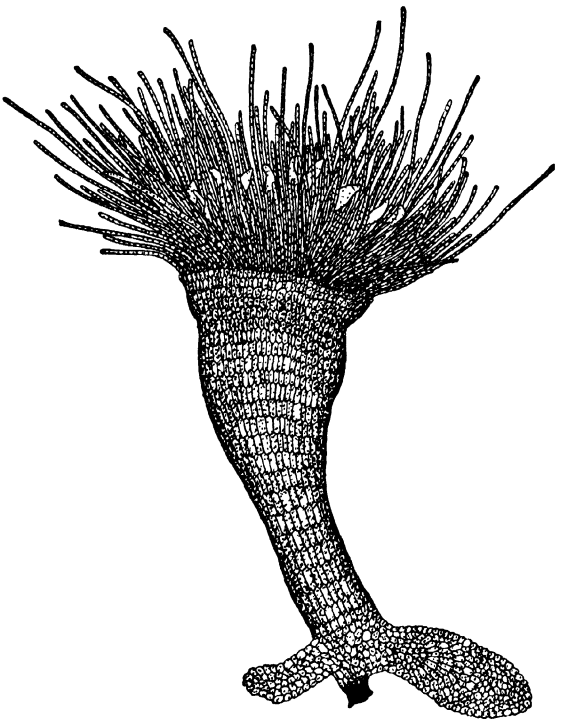


FIG. 246.—*Zodiomyces vorticellarius*. Mature individual. (× 195; *after Thaxter*, 1896.)

Laboulbeniaceae.—The central family which has given the order its name is the largest in the order with about thirty genera, parasitic on most of the groups of insects. The ontogeny has been more fully studied and will be given in detail.

The ascospores are formed in asci, occasionally eight, usually four by the degeneration of four nuclei (Fig. 252, 7 and 8). Very early they are unicellular, later except in *Amorphomyces* dividing into a long basal and short apical cell (Fig. 252, 9). They are oriented in the ascus according to their later bipolar development, with the basal cell uppermost and are surrounded by a gelatinous, sticky sheath, which is usually

characteristically thickened at the base (Fig. 252, 9). At first it provides for the attachment of the spore to the substrate. The plants developing from the ascospores are regularly surrounded by a thin, homogeneous, impermeable membrane, developed from the gelatinous sheath of the ascospore, which by its blackening, often conceals the structure of the plant. It protects the plant from drying out during sudden changes of humidity (even fixatives do not penetrate it well). The ascospores

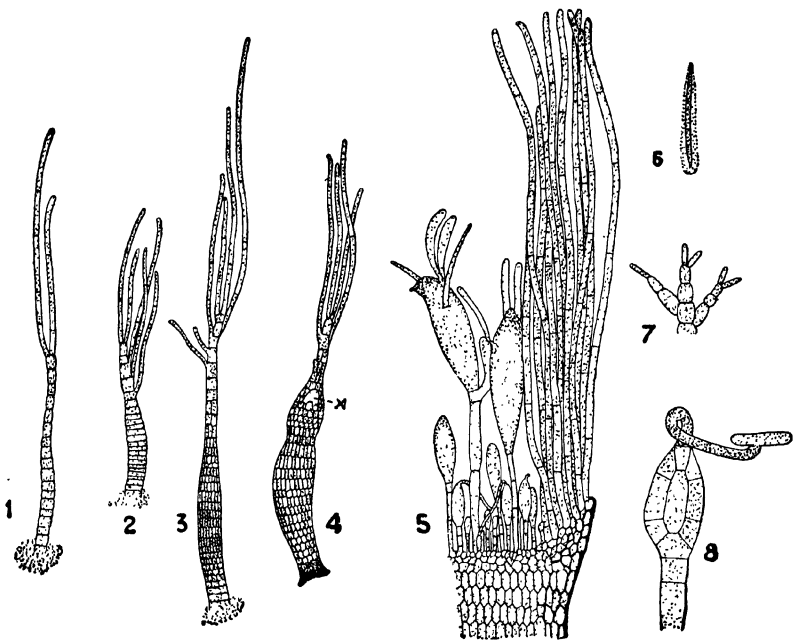


FIG. 247.—*Zodiomyces vorticellarius*. 1 to 4. Young individuals; at *x*, a cavity forms. 5. Section through periphery of mature fructification; at the right, secondary appendages which surround the edge of the cup. On the floor of the cup, antheridia and perithecia in various stages of development. 6. Mature ascospore. 7. Spermatial branch. 8. Young perithecium whose trichogyne has copulated with a spermatium. (1 to 4 × 145, 5, 6 × 260, 7 × 850, 8 × 1,170; *after Thaxter*, 1896.)

are not generally discharged singly but cling together in pairs, thus guaranteeing continuity for the dioecious species. In *Amorphomyces Falagriae* (Fig. 245, 1), generally a male and female stand so close together that they seem to have arisen from the same foot. In *Moschomyces*, the ascospores are discharged in small groups, and the young plants may form small tufts.

If the ascospore reaches its proper host and succeeds in adhering by the basal end, the basal cell divides, cutting off a small basal cell, the foot (Fig. 248, 2). Then the upper cell of the now three-celled plant

begins to develop differently in different genera. *Stigmatomyces Baeri* on the housefly in Europe may be taken as an example with a slightly developed receptacle (Thaxter, 1896).

The apical cell divides by an oblique septum into two cells of which the upper is divided by a second oblique septum into two daughter cells.

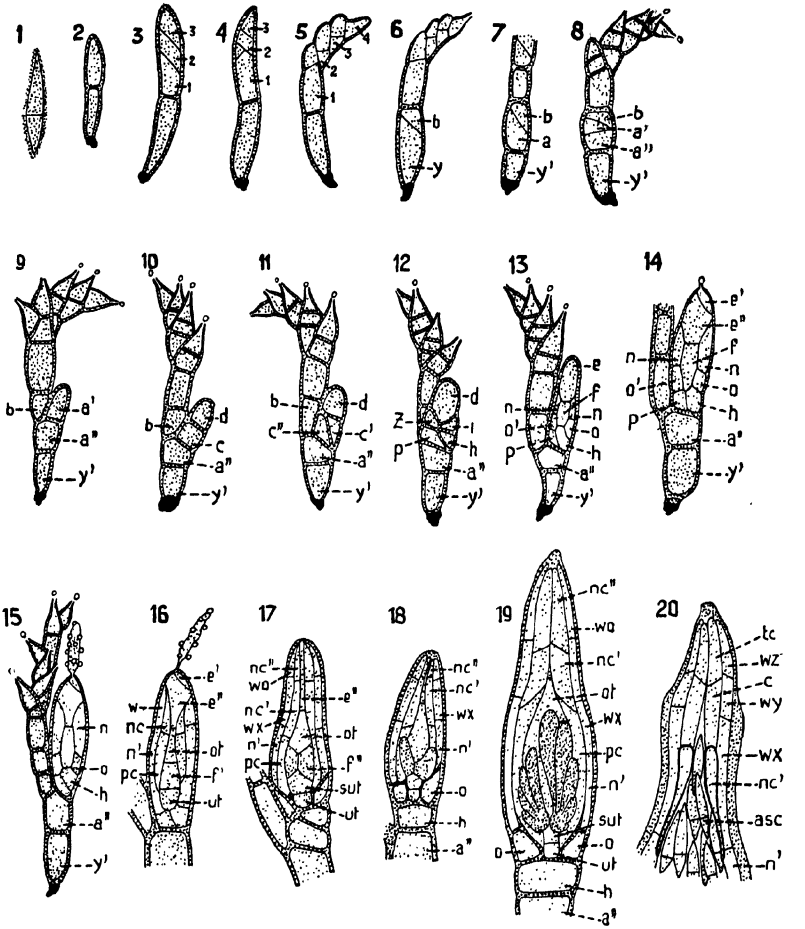


FIG. 248.—*Stigmatomyces Baeri.* Development. (× 340; *after Thaxter*, 1896.)

Thus three daughter cells are formed, which we will number, beginning with the lower, as 1, 2 and 3 (Fig. 248, 3). The lowest cell, 1, divides by an oblique septum, perpendicular to the original one, into a small apical cell and a large basal cell. The new apical cell grows rapidly and pushes cells 2 and 3 somewhat to one side (Fig. 248, 4).

Meanwhile the third cell is again divided by an oblique wall, parallel to the first, so that there are now four cells in the row. Also cells 2 and 3 have divided successively by new oblique walls perpendicular to the first, as earlier happened with cell 1, into a small apical and a larger basal cell. Again these cells increase in size and push still further to the side the series of cells above (Fig. 248, 5).

Meanwhile cell 4 is divided by a septum again so that the cell row has increased to 5. Besides, the apical cell has divided into a tip cell and basal cell; the tip cell functions as a spermogenous cell and discharges tiny bacilliform spermatia, at first naked or only covered by a very thin wall; Gäumann prefers to call them conidia, consequently he calls the flask-shaped antheridium a conidial mother cell from their superficial similarity to the conidia of *Thielavia*.

Meanwhile the basal cell of the ascospore, which had already cut off the foot, has resumed its development. First, it divides by an oblique septum into a small upper cell *b* and a larger lower cell *y* (Fig. 248, 6). Later cell *b* becomes the stalk cell of the appendage and persists without further development.

On the other hand, cell *y* divides into a basal cell *y'* and into cell *a* (Fig. 248, 7) which itself divides into the daughter cells *a'* and *a''* (Fig. 248, 8). The sequence of this division is not absolutely constant. Thus it may also occur that, as in Fig. 248, 7, the basal cell is first cut off and only then do cells *a* and *b* arise as daughter cells of a common mother cell, completing the development of cell *a''*; in common with cell *y'*, it forms the extramatrical part of the vegetative body; with increasing age these cells augment their original length and later, somewhat as indicated for *Stigmatomyces Limnophorae* (*S. Sarcophagae*) (Fig. 249, 2), bear the perithecium in the form of a stipe. This extramatrical part of the thallus in the Laboulbeniales is called the receptacle. In *Laboulbenia e.g., L. Gyrinidarum* and *L. chaetophora*, the walls are formed of two to five layers; outermost, a layer of radially placed plates which degenerate in age to a granular network, and within, several layers of homogeneous, structureless plates penetrated by some thread-like veins.

In contrast to cell *a''*, cell *a'* continues to develop the ascogonia and perithecium. At first it grows upwards and outwards (Fig. 248, 9) and divides into two daughter cells *c* and *d* (Fig. 248, 10); the first forms the primordial cell of the perithecial wall, the latter the primordial cell of the archicarp, the so-called procarp. The cell *c* proceeds first to divide by a more or less oblique wall into two daughter cells *c'* and *c''* (Fig. 248, 11). Cell *c''* elongates and divides into the daughter cells *z* and *p* (Fig. 248, 12). The latter has hereby completed its development; it later forms the stalk cell of the perithecium; the former *z* will divide further. The cell *c'* divides also into upper and lower cells, *i* and *h* (Fig. 248, 12). The lower cell we will call the secondary stipe cell of

the perithecium. It lies directly beside *p*. The cell *i*, however, divides in the plane of the picture into two daughter cells, so that one lies in front and one behind, and hence cannot be shown in the picture. Cells *ii* and *z* begin to grow upwards and surround cell *d*, the primordial cell of the archicarp.

The cell *z* subsequently divides into *o'* and *n* (Fig. 248, 13); one of the cells, *ii* divides similarly into cells *o* and *n*, while the other, here not indicated, divides into a lower and two upper cells. Those three cells, *o*, *o'* and *o''*, not indicated in our figure, which arose from the division of the second cell *ii*, form the true basal cells of the perithecium. They remain undivided while the four cells *n* in time will develop to the four cell rows of the outer perithecial walls.

Meanwhile cell *d* has divided into two daughter cells *f* and *g* (Fig. 248, 13). The former is surrounded by the four cells *n* and the three cells *o*, the latter projects into the open.

The cell *e* cuts off the small tip cell *e'* (Fig. 248, 14) which develops terminally to a trichogyne. In sexually mature individuals, the archicarp consists of three distinct parts which, as far as known, are present in all Laboulbeniales; a trichogyne which in the present example is unicellular, the cell *e''* which is called the trichoporic cell and cell *f* which is called the carpogenic cell, since it forms the true fertile cell.

During this time numerous spermatia have clung to the receptive prominences[1] of the trichogyne, and apparently, as in *Collema crispum*, there occurs a sexual act and nuclear migration; in any case the trichogyne collapses shortly, while the carpogenic cell divides into three daughter cells (Fig. 248, 16), into the superior supporting cell *ot*, the inferior supporting cell *ut* and the middle ascogonium *f'*. This divides again into two daughter cells, a lower *sut* and an upper *f''*. The lower remains unaltered and forms the secondary supporting cell. The cell *f''* divides by longitudinal walls into four daughter cells, of which, in the figure, only the front two are indicated (Fig. 248, 17); these are the four ascogenic cells which successively produce two rows of asci as in any other Laboulbeniales.

Meanwhile the perithecial wall has continued to develop. The three basal cells *o*, *o'* and *o''*, have developed in the interior the four original primary cells *n* of the outer perithecial walls to four new secondary wall cells *n''*, which alternate with the four primary. The outer wall cells *n* divide each into an upper daughter cell *w* and a lower daughter cell *n'*; then the inner wall cells *n''* each divide into a lower daughter cell *pc* and an upper daughter cell *nc* (Fig. 248, 16). The four

[1] Doctor Thaxter informs me that the structures represented on the trichogynes in these figures are not adherent spermatia as formerly supposed, but are receptive prominences of the trichogyne itself, similar to those figured in *Acompsomyces* (Thaxter, 1908, pl. 42, figs. 8 and 12).

cells *nc* become the canal cells, the four cells *pc* the parietal cells. In Fig. 248, 17, the former have divided into an upper daughter cell *nc''* and a lower daughter cell *nc'*; at the same time the outer wall cells *w* have divided into two daughter cells *wo* and *wx*. The perithecium remains a long time in this condition. Before the maturity of the asci, the cells *nc''* divide into four upper cells *tc* and four lower cells *c*; and,

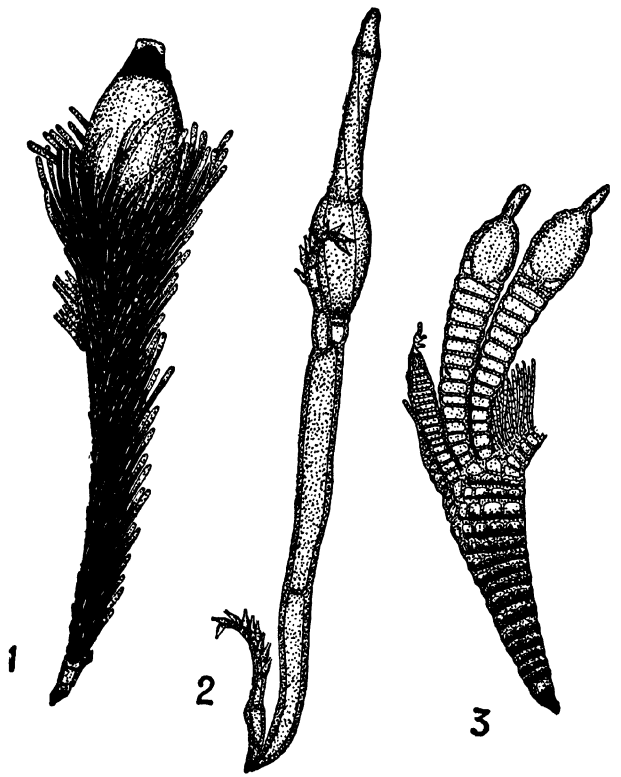


FIG. 249.—1. *Rhachomyces velatus*. Habit; the perithecium has been liberated by pressure on cover glass. 2. *Stigmatomyces Limnophorae*. Normal and dwarf individual where the perithecium aborted. 3. *Kainomyces isomali*. Mature individual. (× 195; *after Thaxter*, 1908.)

the cells *wo* into four cells *wy* and the four *wz* (Fig. 248, 20). The cells *wz* are called lip cells, the cell rows *tc*, *c* and *nc'*, the canal cells; the lowest row *nc'* gradually thicken their walls. The perithecium consists of 37 cells, the primary stipe cell *p*, the secondary stipe cell *h*, and the three basal cells *o*, *o'* and *o''*, the 12 wall cells *n'*, *wx* and *wy*, the four lip cells *wz* the four parietal cells *pc*, and the 12 canal cells *tc*, *c* and *nc'*. The genetic homogeneity of these different cell groups may occasionally be verified in the mature individuals by means of the protoplasmic

connections, as in the Pezizales, etc., (Meyer, 1902, among others) and in *Polysiphonia* in the higher Floridaes (with the exception of the septa of the original perithecial cells, of the trichogyne and the appendages) septa between cells of the same origin show perforations in the middle lamella penetrated by protoplasmic threads.

In the course of this whole development, which takes about three weeks, the perithecium has developed to a large cell body which, as is shown in Fig. 249, 2, in *Stigmatomyces Limnophorae*, projects far beyond the sympodial antheridium and has pushed it to one side. By the pressure of the developing asci, the superior supporting cell *ot*, the second-

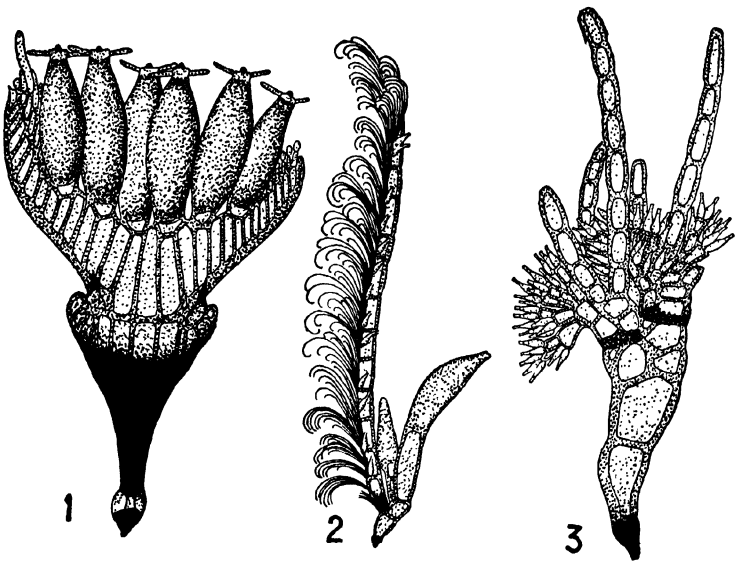


FIG. 250.—1. *Dichomyces biformis*. Mature individual with six, horned perithecia. 2. *Rhizomyces crispatus*. Mature individual. The ends of the appendages are more curved in nature. 3. *Laboulbenia elongata*. Abnormal individual; the perithecium aborted, antheridial appendages borne on the blackened bases where perithecial normally develop. (1 × 400; 2 × 195; 3 × 145; *after Thaxter*, 1896 and 1908.)

ary supporting cell *sut* and the parietal cells *pc* are gradually destroyed; and often even the inferior supporting cell *ut*. The ascus walls disintegrate so that the ascospores *asc* lie free in the perithecial cavity. They are pressed out between the thickened lower canal cells *nc'*, destroy the upper canal cells *c* and *tc*, and are thus liberated between the lip cells *wz*. Individuals which mature in the fall may discharge ascospores through the whole winter into spring.

In other Laboulbeniaceae, numerous variations from this scheme are known. As already mentioned in the introduction, certain forms possess not a foot but a well-developed haustorium. There is also a

great variability in the number of receptacle cells. The majority of genera as *Amorphomyces* (Fig. 245, 1) and *Arthrorhynchus* (Fig. 251, 1) show only two receptacle cells. In other genera, the receptacle may develop to a small, flat cell complex. The perithecial receptacle arises directly from

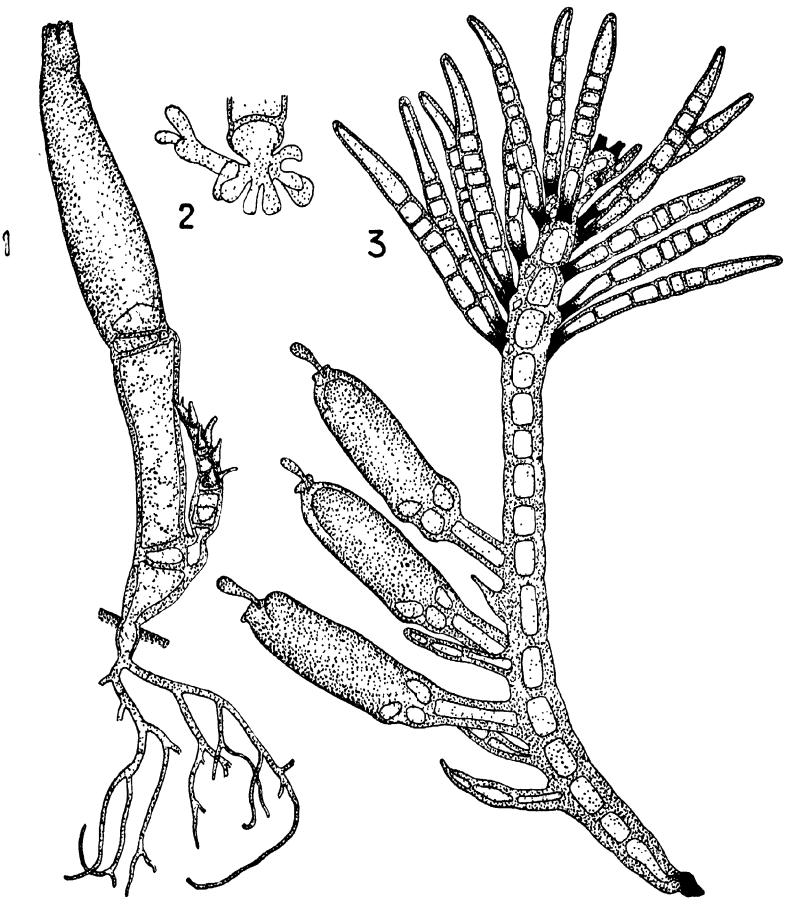


FIG. 251.—1. *Arthrorhynchus Cyclopodiae.* Showing well-developed haustorium. 2. *Rhizomyces ctenophorus.* Haustorium. 3. *Enarthromyces indicus.* Showing three mature and three aborted perithecia. (1, 3 × 195; 2 × 145; *after Thaxter,* 1896 and 1908.)

the basal cell of the germinating ascospore; hence it is called the primary receptacle. In *Dichomyces* (Fig. 250, 1) the secondary receptacle is a direct continuation of the primary and hence is not recognizable as such. In *Herpomyces,* the secondary receptacle crawls along the substrate, so that the fertile secondary branches seem to branch from a stroma. In

H. Periplanetae the basal cells of the primary and secondary receptacles develop fine rhizoids which penetrate the host wherever they are in contact with it.

In *Stigmatomyces*, the appendages are only slightly developed (Fig. 248, cell *b*) and may grow from either the cells of the ascospore or their derivatives; those from the upper cell of the ascospore are called primary appendages, all others secondary appendages. They attain their greatest development in some species of *Rhachomyces* where they seem to surround the whole plant (Fig. 249, 1) and occasionally project above the perithecium. They probably serve for protection and the holding of condensed water.

In most genera the antheridia are localized in a definite manner in certain positions on the appendage, *e.g.*, at the base, somewhat as in *Rhizomyces crispatus* (Fig. 250, 2). These simple antheridia may stand in a definite order, as in vertical rows in *Stigmatomyces*, three vertical rows in *Idiomyces*, four in *Arthrorhynchus*, or they may be entirely irregularly arranged and (as in certain cases where the perithecium fails to develop) may subsequently multiply in number (Fig. 250, 3). In still other species, as *Laboulbenia Gyrinidarum* and *L. chaetophora*, no spermatia have been observed.

The Laboulbeniaceae show some variations in perithecial development. The direction of the rows of wall cells may twist in age (Fig. 249, 2), or the perithecial tip may bear appendages known as trigger organs (Fig. 250, 1) or the number of wall cells in a row may exceed four (in *Moschomyces* and *Compsomyces* five, in other genera entirely variable).

The archicarps of the Laboulbeniaceae have very uniform relationships. In all forms studied, the division into the trichogyne, trichophoric cell and carpogenic cell has been observed. Often the trichogyne attains a higher development than in *Stigmatomyces*. Thus in *Amorphomyces*, it is still unicellular, but definitely lobed (Fig. 245, 1). In most other genera it is multicellular, at times much branched, either straight, more or less as in *Laboulbenia Gyrinidarum* (Fig. 252, 1) or helical, as in *Compsomyces verticillatus*. How fertilization and nuclear migration occurs in these tufted trichogynes, is still unknown. In some of these forms with complicated trichogynes, as *L. Gyrinidarum*, spermatia have not been seen and the asci perhaps may develop parthenogamously as in *Polystigma rubrum* and various species of Pezizales.

These relationships were cytologically studied in two very closely related species, *Laboulbenia Gyrinidarum* and *L. chaetophora* (Faull, 1912) on the elytra of *Gyrinus* sp. Fig. 252, 1 shows the archicarp mature for fertilization; it suggests *Stigmatomyces Baeri* (Fig, 248, 5) and consists of carpogenic cell, trichophoric cell and trichogyne. All of these cells in the Laboulbeniales are uninucleate. The nuclei of the carpogenic cell and the trichophoric cell (Fig. 252, 2) each divides. The septum is dis-

solved and the four nuclei lie in one cell (Fig. 252, 3). Now the basal cell is formed, so that the lowest of the four nuclei is separated in a restored trichophoric cell. The middle nuclear pair increases in size and

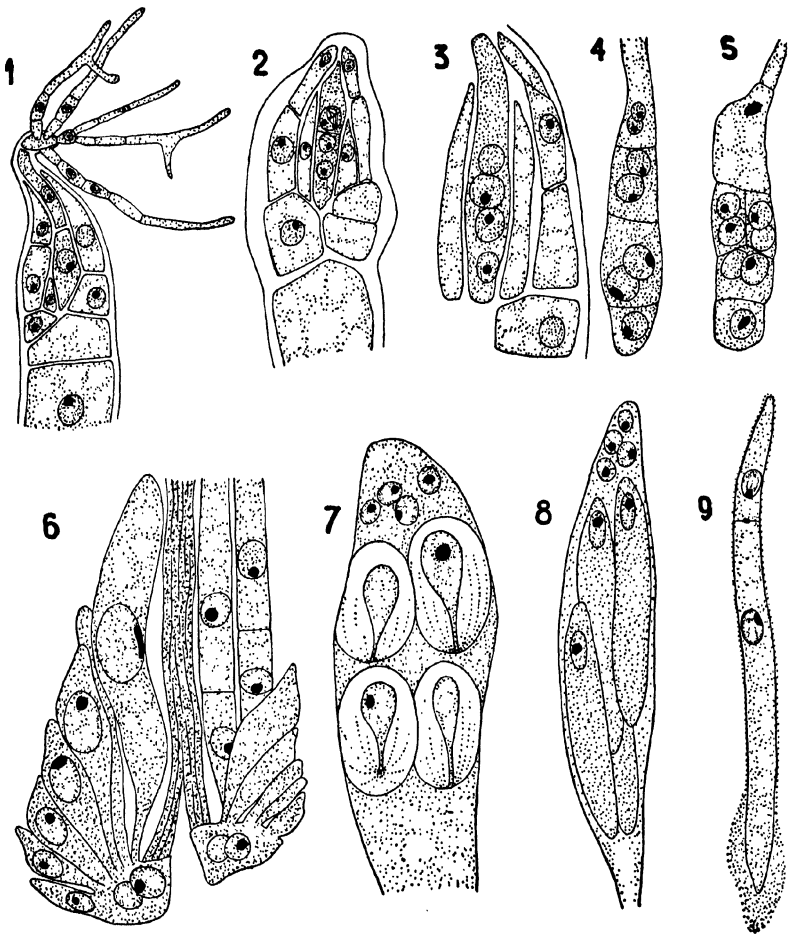


FIG. 252.—Development of asci in *Laboulbenia Gyrinidarum* and *L. chaetophora*. 1. Mature archicarp. 2. The nucleus of the carpogenic cell has divided, that of the trichophoric cell is dividing. 3. Plasmogamy completed. 4. Row of cells consisting of the basal uninucleate supporting cell, the basal binucleate supporting cell, the fertile cell and the upper binucleate supporting cell. 5. Longitudinal section of ascogenous cell. 6. Two active ascogenous cells. 7 to 9. Development of ascospores. (1, 4 × 300; 2, 3, 5 × 400; 6 × 900; 7, 8 × 1,200; 9 × 600; *after Faull*, 1912.)

divides conjugately. The upper cell becomes a sterile cell and the lower alone remains fertile. Its nucleus divides again and cuts off a binucleate fertile cell (Fig. 252, 4). Hereupon it may form the fundament of the

asci or first divide longitudinally (Fig. 252, 5). The fundament of the asci develops by a conjugate division of the ascogenous cells; a daughter pair migrates into the young ascus, the other daughter pair remains in the ascogenous cells. This process is repeated (Fig. 252, 5). The fusion of the carpogenic cell and trichophoric cells probably is a plasmogamy similar to that of *Polystigma rubrum*.

Of other differences between the Laboulbeniales so far known and the *Stigmatomyces* type, only the variation in number of ascogenous cells will be mentioned. While there are four in *Stigmatomyces* and two in

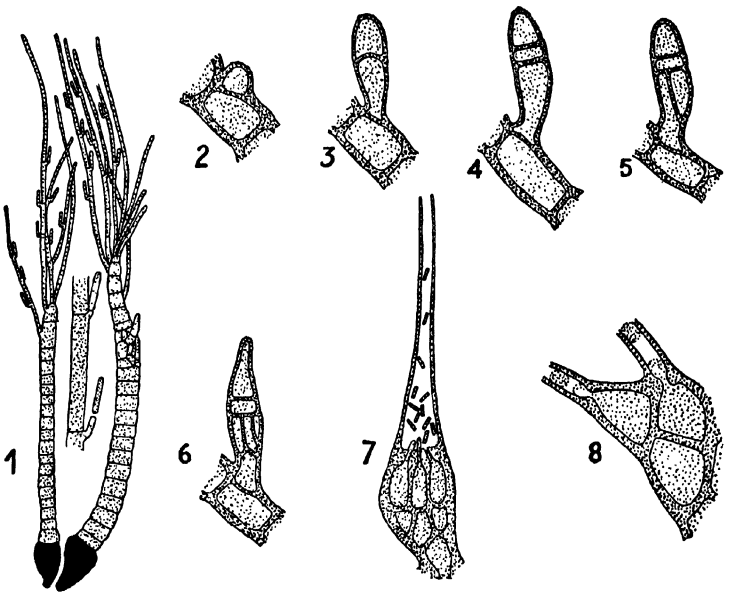


FIG. 253.—Types of Antheridia. 1. *Rhynchophoromyces rostratus*. 2 to 6. *Dimeromyces adventitiosus*. 7. *Dimeromyces africanus*. 8. *Stigmatomyces Baeri*. (1 × 200, inset × 850; 2 to 6 × 725; 7 × 700; 8 × 1,840; *after Thaxter*, 1898 and 1924.)

Laboulbenia, there is only one in *Amorphomyces*, and in *Polyascomyces* about thirty-two; in the latter the ascogenous cells form a sort of placenta from which the asci develop.

Peyritschiellaceae.—In this family the antheridial cells have united into a specialized organ and do not discharge their spermatia directly from their opening, but extrude them into a common cavity from which they are liberated (Fig. 253, 2 to 7), hence they are called compound antheridia.

This family contains about 25 genera, some of them very large, and seems to reach the height of its development in the tropics.

Rickia may be taken as an example of the Peyritschiellaceae with a highly developed and variable receptacle. While the axis is often simple,

it may be branched, either normally (as in *R. dichotoma*, Fig. 255, 4) or as the result of injury. The cells of the receptacle, exclusive of the smaller cells which are separated from them and which give rise to antheridia or secondary appendages, may be less than 10, as in *R. Sylvestri*, (Fig. 254, 1) while in *R. Discopomae* (Fig. 254, 7) and *R. dichotoma* there may be more than 100. Their number is usually somewhat indeterminate.

The primary axis is usually triseriate, consisting of two marginal series, that on the perithecial side called the anterior; that on the opposite

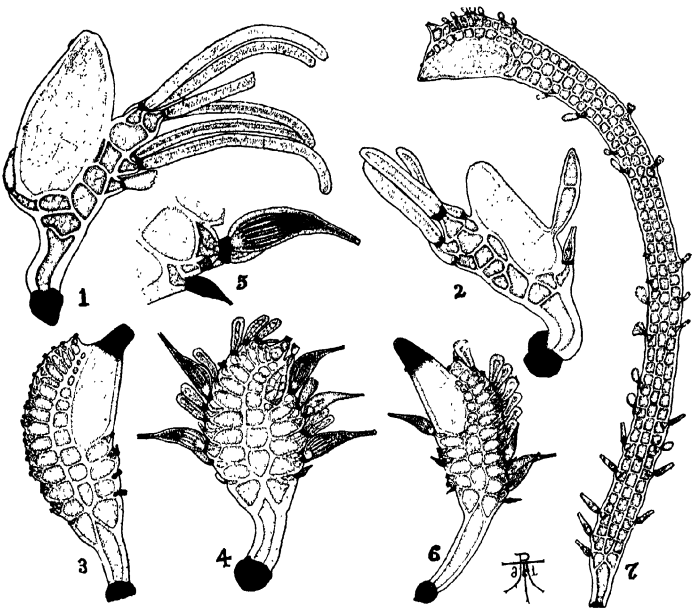


FIG. 254.—*Rickia Sylvestri*. 1. Mature individual. 2. Showing aborted perithecium with secondary one proliferating from its base. *Rickia macrandra*. 3. Old individual denuded of antheridia and appendage. 4. Young one with five large, and one small, antheridia. 5. Antheridia of 4 enlarged. 6. Mature individual with dimorphic antheridia. *Rickia Discopomae*. 7. Mature individual. (*After Thaxter*, 1926.)

side, definitely related to the primary appendage, called the posterior, the third, median or axial series which may consist of a single cell, as in *R. Sylvestri* (Fig. 254, 1), or may be as highly developed as in the other two (*R. Discopomae*, Fig. 254, 7) or may be wholly absent in the biseriate types (Fig. 257, 4) (formerly distinguished as *Distichomyces*). The axial series is normally associated with the inner margin of the perithecium, sometimes extending far below the latter, as in *R. admirabilis* (Fig. 256, 4) often reaching nearly to its apex or even higher than the posterior series in *R. elegans*. Ordinarily the cells of the axial series produce neither antheridia nor appendages, although in *R. pallida* (Fig. 255, 1)

and *R. encymonalis* (Fig. 256, 5) appendages may develop from the distal cells. Thus the receptacle is a flat ribbon lying upon the substrate, usually attached by a unicellular, abruptly differentiated stalk with the usual black foot.

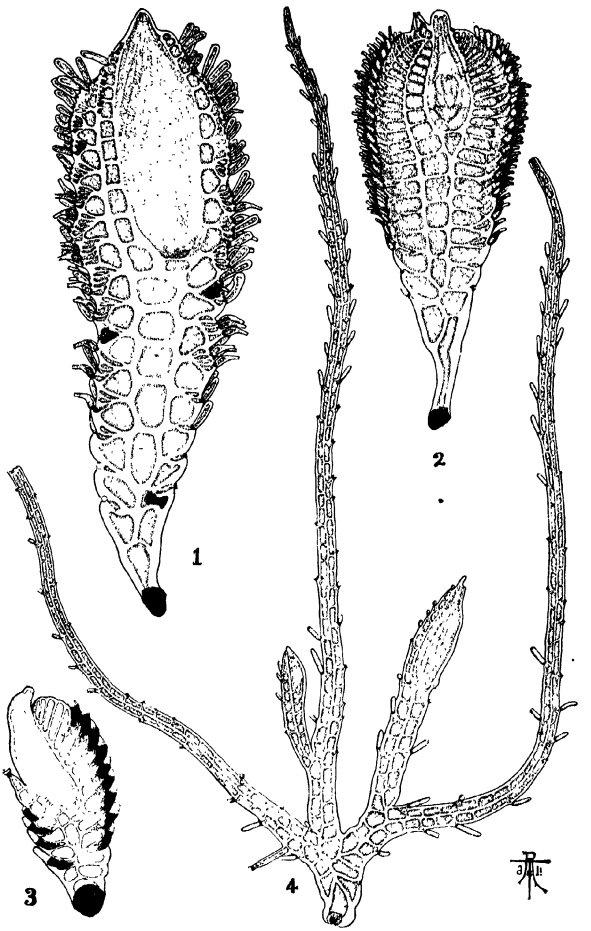


FIG. 255.—1. *Rickia pallida.* Blackened cells, disorganized. 2. *Rickia papuana.* Immature individual. 3. *Rickia introversa.* 4. *Rickia dichotoma.* Showing two parallel axes. (*After Thaxter*, 1926.)

Growth may be either apical or trichothallic as found in the basal cells of the brown and red algae or a combination of both types. The terminal cell of the germinating spore develops a primary appendage with a two-celled base. The basal cell divides, cutting off the stalk cell with the foot and leaving the upper cell from which all secondary growth

proceeds. This cell divides by an oblique wall to an anterior lower and a posterior upper cell, both of which then divide transversely, the two lower of the cells thus formed corresponding to the basal pair of the marginal cells in the adult. The anterior of the two upper cells continues

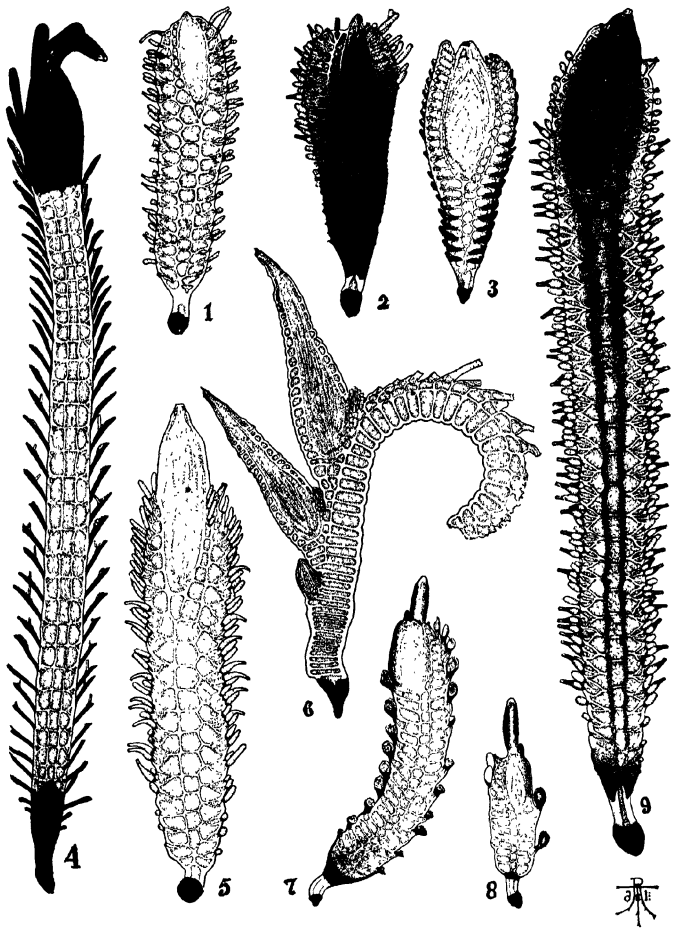


FIG. 256.—1, 2. *Rickia circumdata*, mature individuals. 3. *Rickia inclusa*. 4. *Rickia admirabilis*. 5. *Rickia encymonalis*. 6. *Tettigomyces acuminatus*. 7, 8. *Rickia rostellata*. 9. *Rickia coptengalis*.

to divide transversely until the normal number of cells characteristic of the anterior series has been reached. The posterior of these two upper cells, although it may divide transversely, eventually divides longitudinally, the inner of the resulting cells organizing the axial series by repeated transverse division, while the outer similarly organizes the posterior series.

When no longitudinal division occurs, a biseriate axis results, as in *R. biseriata* (Fig. 257, 4) and *R. dichotoma* (Fig. 255, 4). These biseriate forms may be regarded as more primitive, since in cases of injury or perithecial abortion, secondary axes which develop from them adventitiously and might be expected to show an atavistic tendency, are biseriate. Occasionally apparently normal individuals of the biseriate type may develop in species which are ordinarily triseriate.

At a definite stage of development, a longitudinal division occurs in the terminal cell of the anterior series. Of the two resulting cells, the inner becomes the primordium of the perithecium while the other either ceases its activity and subtends the perithecium, as in *R. rostellata* (Fig. 256, 7 and 8), or continues to divide transversely until it reaches the apex of the developing perithecium, as in *R. circumdata* (Fig. 256, 1 and 2). Similarly, the posterior series may end below the base of the primary appendage which at maturity may be subtended by the posterior terminal cell as in *R. coptengalis* (Fig. 256, 9), or it may push aside the primary appendage and continue along the edge of the perithecium, as in *R. biseriata* (Fig. 256, 4 and 7). Such a case illustrates the combination of trichothallic and apical growth, in which growth is trichothallic below the primary appendage and apical beyond it.

The cells of the outer series may cut off one or two smaller cells, by single or successive separation downward from their upper, outer angle, which organize either single secondary appendages or antheridia. The relative position of the appendiculate cells may not always be the same, even in the same individual; they may be vertically superposed, horizontally seriate or separated from the mother cell in such a way that they lie crowded in different radii of the same circumference. A slight protrusion is abjointed and develops a simple unicellular appendage, while the septum becomes variously blackened and constricted.

The antheridium begins to develop exactly as an appendage. The septum occasionally remains unmodified and the antheridium immersed. The primary division of the original appendiculate cell separates an inner stalk cell from an outer which organizes the venter and neck of the antheridium. In the venter a small basal cell may be seen, above which a group of two or more antheridial cells discharge spermatia through minute pores into the main cavity of the neck. These are evanescent, the whole content of the antheridium disorganizes, leaving a continuous cavity which might be mistaken for the simple cavity of the Laboulbeniaceae.

In *R. macrandra* (Fig. 254, 6), besides the free antheridia of the normal type, giant antheridia (Fig. 254, 4 and 5) are produced in which numerous elongate antheridial cells arise directly from a hemispherical basal cell of the venter, arranged in a subterminal whorl. In this type the sperms are discharged in great numbers and pass through short pores into a chamber

formed by the expanded base of the neck, much as in the more highly compound types of other genera.

In some species, as *R. dichotoma* (Fig. 255, 4), *R. inclusa* (Fig. 256, 3), *R. introversa* (Fig. 255, 3) and related species, there is no indication of

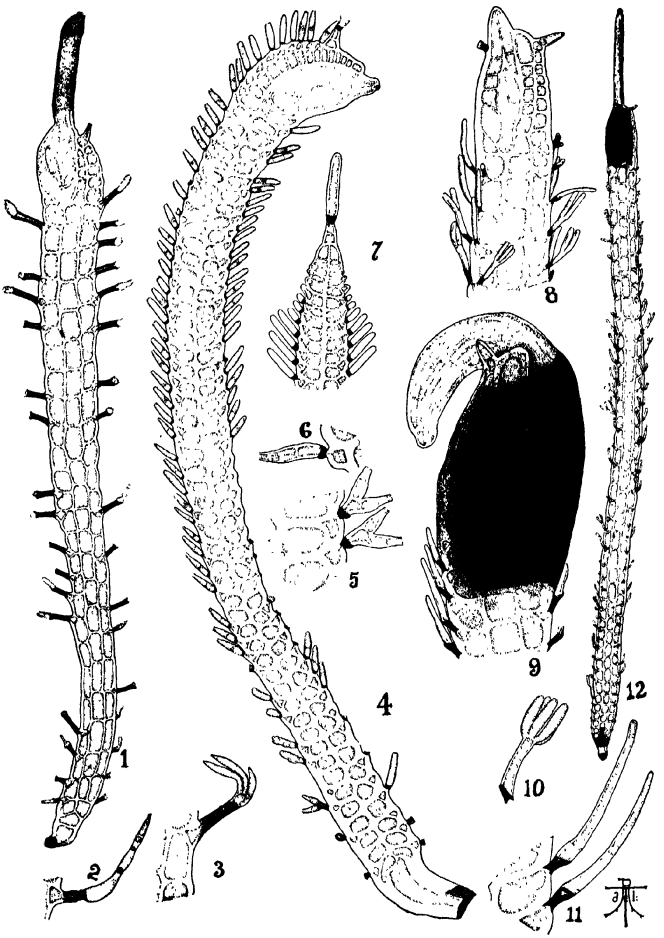


FIG. 257.—*Rickia rostrata*. 1. Mature individual. 2. Simple secondary appendage. 3. Branched secondary appendage. *Rickia biseriata*. 4. Mature individual. 5, 6. Paired and single antheridia. 7. Apex of young individual, showing trichothallic growth. *Rickia Coelostomalis*. 8. Tip of young individual, showing cell arrangement. 9. Perithecium with recurved neck. 10. Appendage with umbellate terminal branchlets. 11. Two normal single, secondary appendages. 12. Mature individual. (*After Thaxter*, 1926.)

antheridial formation; in *R. Sylvestri* only one is produced while in *R. papuana* (Fig. 255, 2) and *R. coptengalis* (Fig. 256, 9) they are very numerous, often a hundred or more in a single individual. In other

species, as *R. Coelostomalis* (Fig. 257, 8 to 11) and *R. rostrata* (Fig. 257, 1), while functional antheridia have not been seen, vestigial structures were observed.

Perithecial development is similar to that of *Stigmatomyces Baeri*. The trichogyne is often characteristically branched with slightly swollen

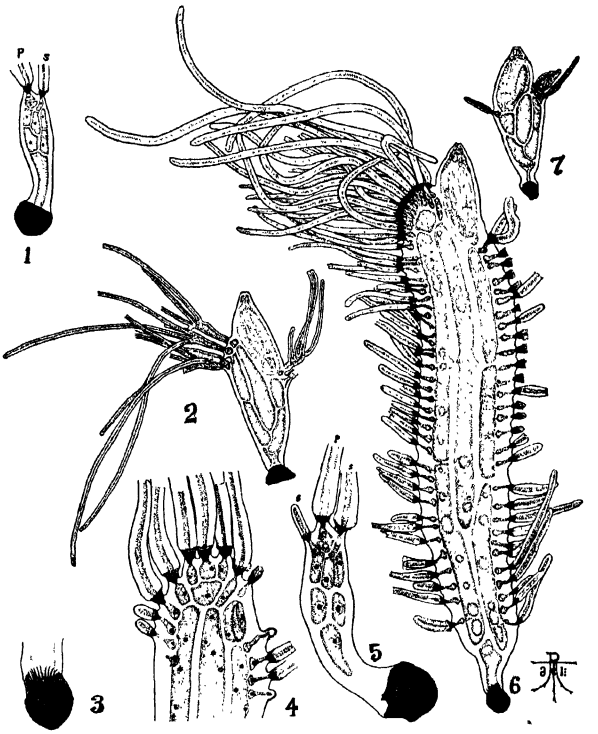


FIG. 258.—*Diaphoromyces marginatus*. 1. Young individual showing the relation of the posterior series to the two-celled base of primary appendage (left). 3. Foot of adult showing striations. 4. Termination of young axis showing formation of the basal cells of secondary appendages by nuclei, at different stages. 5 Young individual showing primary appendage *p* and secondary appendages *s*. 6. Fully mature individual. *Diaphoromyces Lispini*. 2. Form with branched and highly developed appendages, from Trinidad. 7. Smaller simpler type from California. (*After Thaxter*, 1926.)

extremities. Its persistent base is usually evident on the anterior margin of the perithecium.

Diaphoromyces (Fig. 258) has recently been separated from *Rickia*, on account of the peculiar ontogeny of its secondary appendages, which are successively developed from above downward by the activities of large free nuclei in the cells of the lateral series (Fig. 258, 4). One of its nuclei takes its position against the inner surface of the wall and together with a small portion of protoplasm organizes a small cell, surrounds itself

with a wall firmly attached to the inner surface of the wall of the mother cell. This small cell which ultimately becomes the basal cell of the appendage then perforates the wall of the mother cell, growing outward through it by a narrow extension of its protoplasm, which, finally reaching the outer surface, forms there a walled prominence from which the appendage is organized.

In some species of *Ilytheomyces*, (Thaxter, 1917) *Chitonomyces* and various other unrelated genera, "trigger" organs develop in positions which affect the tension within the perithecium, on contact with another host

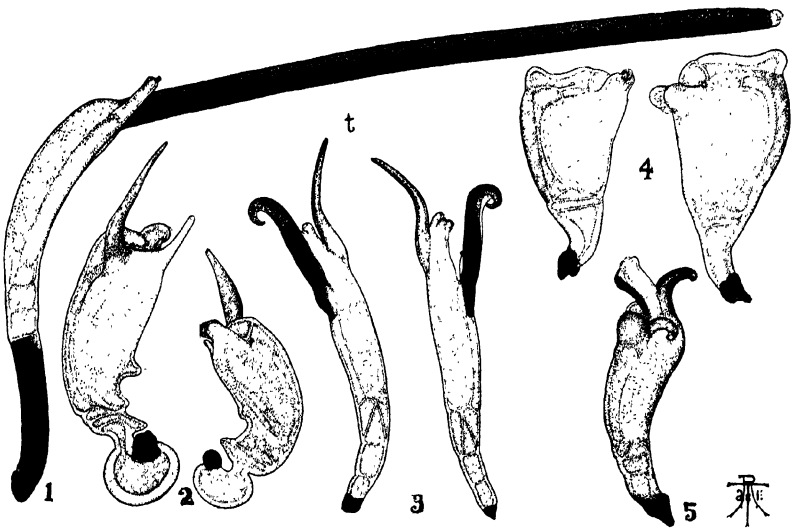


FIG. 259.—1. *Chitonomyces longirostratus*, showing tip of perithecium highly developed and functioning as a trigger organ. 2. *Chitonomyces oedipus*, showing trigger organs. 3. *Chitonomyces japanensis*. 4. *Chitonomyces introversus*. 5. *Chitonomyces cerviculatus*. (*After Thaxter*, 1924.)

or any firm object, in such a manner as to induce a sudden discharge of spores *e.g.*, *C. oedipus*, *C. japanensis*, etc. (Fig. 259, 2 to 5). In *Chitonomyces longirostratus* (Fig. 259, 1) the cells of the perithecial tip are elongated into a slender, indurated tube. At the impact with another host, slight bending of the tube will produce a very great compression of the perithecium and cause an immediate ejection of spores while the chance of infection is greatest. With the degeneration of the ascus as a mechanism for violent discharge, its function seems to have been assumed by the whole perithecium.

In *Trenomyces*, the basal cell of the receptacle directly penetrates the host without the formation of a differentiated foot, although this region may sometimes be colored. The intruded rhizoid swells more or less abruptly beneath the integument, so that the individual is firmly

held in place. From this enlargement a single simple rhizoid in *T. Lipeuri*, or many branching ones in *T. histophtorus*, make their way into the body substance. The sub-basal cell, by the formation of tangential walls, separates a variable number of small cells which may multiply variously by division, even organizing definite short axes with growing points in *T. Laemobothrii;* and, as a result, the original cell may become more or less corticated. The process is more definite in *T. Lipeuri* in which these cells are comparatively larger and more regular, developing sidewise to form a pulvinate series.

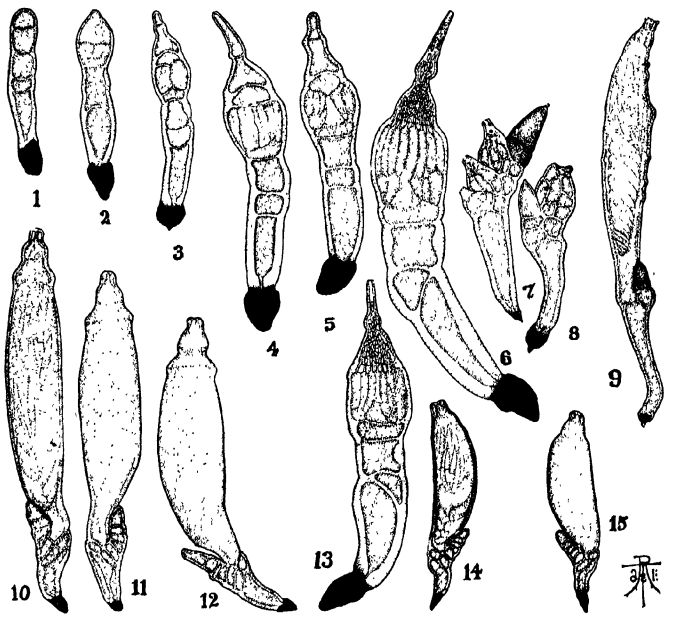


FIG. 260.—*Polyandromyces Coptosomalis.* 1 to 6. Development of male. 10 to 12. Mature females. 13 to 15. Male and two females of var. minor. *Nycteromyces streblidinus.* 7. Mature male. 8. Young female. 9. Mature female. (*After Thaxter*, 1924.)

From a variable number of these cells, single-stalked perithecia arise in the female or antheridia in the male; of which there may be from one or two to more than a dozen in a single individual. The perithecia and antheridia closely resemble those of *Dimeromyces*, the walls of the basal cells in the former being absorbed at an early period so that the cavity of the highly developed stalk cell becomes continuous with that of the ascigerous cavity. In male individuals the cortication is usually much less complicated; and the cells which give rise to the stalked, compound antheridia much like those of *Dimeromyces* may be separated directly from the sub-basal cell without secondary division, as in *T.*

circinans. In an undescribed hermaphrodite genus from the old world tropics, a similar general habit occurs, the sub-spherical receptacle penetrating the host by means of rhizoids and forming perithecia and simple antheridia in a somewhat similar manner.

The development of a compound antheridium may be seen in the dioecious *Polyandromyces Coptosomalis* of the Dimorphomyceteae (Fig. 260, 1 to 6). In the male, the basal segment divides but once, forming a two-celled receptacle, while the distal segment forms three cells which correspond to the three primary regions of the antheridium; the stalk cell which divides no further, the terminal cell which becomes pointed and forms the efferent region, and the middle cell which separates a single cell above and below, the secondary stalk cell. The middle cell divides and proliferates to form the very numerous antheridial cells whose necks push up through the upper cell which is destroyed and discharge their spermatia into the common cavity formed by the resorption of the cells of the efferent region, leaving only their outer walls.

In the corresponding female individual (Fig. 260, 10 to 12), the upper cell of the spore remains a simple, two-celled, primary appendage, resting on the uppermost of four cells which are formed by oblique division of the basal cells of the spore. The single perithecium is ordinarily developed from the second cell below.

In *Nycteromyces streblidinus*, the antheridia are formed in a series from the basal cell of the spore, while the distal cell remains a two-celled primary appendage (Fig. 260, 7); in the female a solitary perithecium is formed from the upper of the two cells produced by the basal cell (Fig. 260, 8 and 9).

In *Tettigomyces*, the antheridium may be clearly differentiated, as in *T. Gryllotalpae* (Fig 261, 8) and *T. africanus* (Fig. 261, 1 to 3), with the development of many antheridial cells; or it may be represented by a small, undifferentiated group of cells at the base of a highly developed, copiously branched and otherwise sterile appendage; while in *T. chaetophilus* (Fig. 261, 7) no antheridial cells have been observed.

In *T. africanus* (Fig. 261, 3) the antheridia empty through short necks into a central cavity, filled with spermatia, but a definite opening for discharge from the cavity has rarely been seen. Such openings are irregular and seem to be the result of rupture or degeneration rather than a definite pore such as found in *Eucantharomyces*, *Cantharomyces* or *Haplomyces*. Local disorganization, followed by general disintegration of the antheridial cells occurs as development progresses, while in allied species, as *T. vulgaris*, *T. gracilis* (Fig. 261, 6) and *T. intermedius* (Fig. 261, 4 and 5), such degeneration is complete at maturity, and may involve the whole appendage in *T. vulgaris* (Fig. 261, 9 to 12). The double rows of antheridial cells arise as paired branchlets from marginal cells of a typical appendage, as the result of the activity of a corresponding

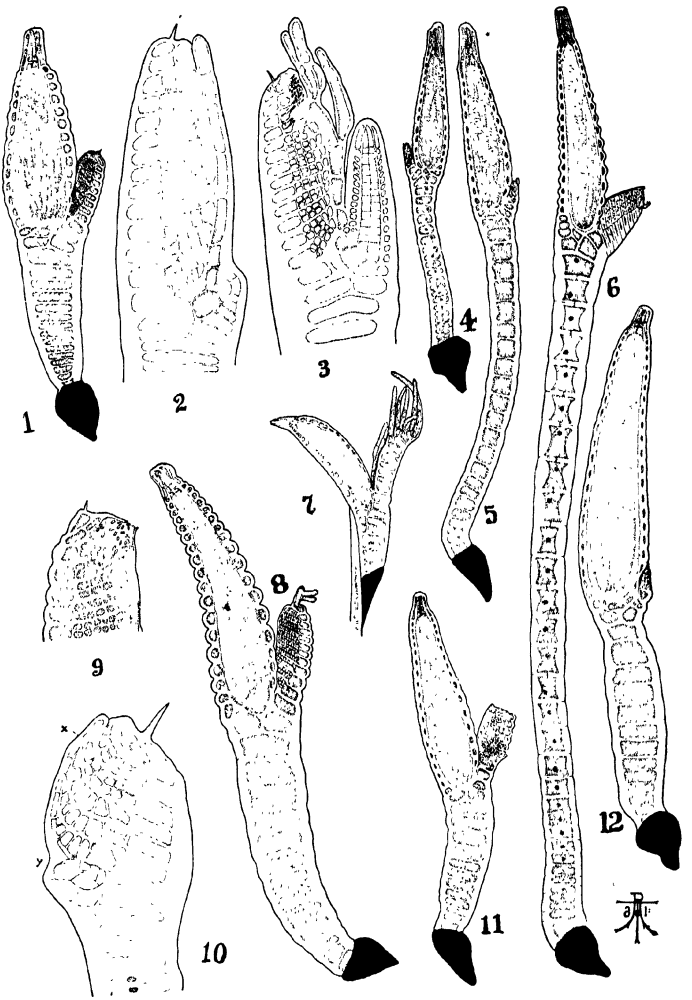


FIG. 261.—*Tettigomyces africanus*. 1. Mature individual. 2. Young antheridium showing relation of adnate trichogyne to antheridial cells and carpogenic cell. 3. Older antheridium; the adnate trichogyne with two free branchlets seen sidewise, and showing necks and discharging spermatia. 4, 5. *Tettigomyces intermedius*, showing the antheridia disorganized. 6. *Tettigomyces gracilis*. 7. *Tettigomyces chaetophilus*, showing free trichogyne. 8. *Tettigomyces Gryllotalpae* 9. *Tettigomyces vulgaris*, showing the tip of antheridial appendage beginning to disorganize and free spermatia. 10. Distal portion of young individual showing terminal spine. Adnate trichogyne, *x*; ascogonium, *y*; young antheridium not fully mature, paired daughter cells below indicating intercalary division. 11. Small individual; antheridial appendage partly disorganized. 12. Large individual with antheridial appendage completely disorganized. (*After Thaxter*, 1926.)

number of terminal cells which cut off basal segments successively. Later they usually divide once, resulting in the association of antheridial cells in pairs (Fig. 261, 9 to 10). The opposite series, arching somewhat, become separated by a space which forms the central chamber into which the spermatia are discharged. In *T. africanus* the trichogyne develops at the same time with the antheridial branchlets and is ordinarily in close contact with them, perhaps in actual contact with the cavity containing the spermatia (Fig. 261, 2). Fertilization might thus occur directly from this cavity, making an actual discharge unessential. This possibility is further suggested by the fact that the exposed portions of the trichogynes are relatively thick-walled, without the usual thin-walled receptive region.

Where no individualized antheridium is produced, the appendage becomes more or less indeterminate in growth, producing a variable number of sterile branches, as in *T. acuminatus* (Fig. 256, 6). In *T. chaetophilus*, (Fig. 261, 7), which produces no visible antheridial cells, there has been seen a trichogyne, sometimes found between the perithecium and the base of the appendage.

Since there is such complete disagreement in the interpretation of many phenomena in this group between Gäumann and Thaxter, in the following discussion, I have attempted to present accurately Gäumann's views and Thaxter's unpublished criticism of them.

In the Laboulbeniales the asterinoid habit has become most strongly developed; but it has undergone extensive morphological degeneration owing to extreme xerophytism. Biologically, they seem to have undergone a development from endo- to complete ectoparasitism, like that we have met in the Perisporiales and Sphaeriales. A few species, as *Trenomyces histophthorus* on *Mallophaga*, are endoparasitic, like *Leveillula taurica* of the Erysiphaceae and *Lanomyces tjibodensis* of the Perisporiaceae, and with their well-developed haustoria penetrate the whole fatty tissue of the host. Other forms, as *Dimeromyces rhizosporus*, *Ceraiomyces Dahlii* and *Arthrorhynchus Cyclopodiae*, correspond to the *Phyllactinia* type of the Erysiphaceae; they form richly branched, intramatrical haustoria which spread only in the immediate vicinity of the point of infection. Other forms, as *Rhizomyces ctenophorus* and *Moschomyces insignis*, penetrate the chitinous integment of the host and form a lobate haustorium on its interior (Fig. 251, 2). In most species the intramatrical portion of the thallus is reduced to an ungulate haustorium, the black foot, which is let into the integument of the host, goes no further into the interior of the body and apparently takes its nourishment through the host integument (Fig. 251, 3). Analogies to this relationship are rarely known in fungi; one was earlier described for *Harpochytrium Hyalothecae* (Fig. 23, 1); another may be seen in Fig. 262, 1. On the basis of the observation that the insects suffer no serious injury and the assumption that a sufficient intake of nourishment through the integument is impossible, the idea has been expressed that the purely ectoparasitic Laboulbeniales are only saprophytes like the epiphytic Sphaeriales of the *Limacinia–Teichospora* type. This idea is hardly correct, since many species are adapted to definite genera of insects.

It seems rather a question of end forms of an asterinoid developmental series in which the step from ectoparasitism to epiphytism is small, as in the Erysiphaceae.

That the food is not rich may be assumed from the small size of most species, which have comparatively few cells. That they are xerophytic is immediately clear if one considers that many Laboulbeniales live on dry legs and elytra of beetles. Physically, their habitat may be damp, as in species on aquatic and swamp insects. Physiologically, the point of food intake is very dry.

The Laboulbeniales, as all the other asterinoid groups, must have undergone an exceptionally far-reaching degeneration; in contrast to the simplicity of the thallus, there is an astonishingly high development of sexual organs and fructifications. The critical point lay in the ectoparasitism on insects, whose leveling influences have been felt by other entomogenous Ascomycetes and imperfecti; many of them also show a Laboulbenial habit as a convergence phenomenon (Thaxter, 1914, 1920). The meaning of these observations is controversial. Are the Laboulbeniales reduced Florideae and their spermatia really spermatia or are they reduced Pyrenomycetes and, therefore, their spermatia are really only originally conidia? To answer these questions which are of fundamental meaning for the phylogenetic derivation of Ascomycetes and fungi in general, and not to anticipate, the discussion of the Laboulbeniales was postponed to the close of the class, although it is completely isolated there.

Their derivation from the Florideae is suggested by the habitual similarity of the Laboulbeniales to some parasitic red algae, and by the type of fertilization by spermatia, which in the endogenous forms are at first surrounded by a very thin membrane. This hypothesis is wrecked in the morphology of the gonotoconts, the asci. It seems improbable that so highly a specialized organ which as regards the free cell formation of its daughter cells, the ascospores, depends upon such definite phylogenetic conditions (coenocytic gametangial copulation, privileging of certain sexual nuclei) could suddenly arise in the short distance from the Florideae to the Laboulbeniales.

If one rejects this possibility and regards the Laboulbeniales as reduced Pyrenomycetes, one is obliged to seek another explanation for the antheridia. The exogenous spermatia of *Zodiomyces vorticellarius* (Fig. 247, 7) and *Rhynchophoromyces rostratus* (Fig. 253, 1) and for the oidia of some species of *Ceratomyces* might be explained as conidia although their germination is still unknown. Morphologically, they are undoubtedly conidia. In any case it is noteworthy that at least in *Zodiomyces vorticellarius*, and probably in *Tettigomyces vulgaris*, as in *Collema pulposum*, they must be sought for by the trichogyne. Thus they must have undergone secondarily a definite sexual differentiation.

The interpretation of the endogenous spermatia is more difficult. In *Stigmatomyces Baeri* they are formed long in advance of the formation of ascogonia (Fig. 248, 8) and their production is continued throughout the life of the plant, even to old age, when the perithecia have finished development and are discharging ascospores. If one wished to explain this spermatial formation on the young plants as extreme protandry, the continuation of spore formation past perithecial maturity must be confusing; such behavior is shown only by imperfect forms, not antheridia.

It is equally confusing that the antheridia may arise from either cell of the germinating ascospore, while the ascogonia arise only from the basal cell. It must appear still more unusual that in *Coreomyces* any cell in any appendage may form spermatia. Such a relationship argues for conidial formation, not for antheridia.

Similar considerations arise in the dioecious forms, the Dimorphomyceteae of the Peyritschiellaceae and the Amorphomycetae and Herpomyceteae of the Laboulbeniaceae. It may be granted that a figure such as we have for *Amorphomyces Falagriae* argues strongly for the conception we reject here: we have male and female plants, the former form spermatia, the latter ascogonia, which are fertilized by spermatia. The two sexes remain connected in pairs because in the ascus the sexually different ascopores already cling together. Unfortunately, this group has not been studied cytologically.

Against this interpretation two objections may be raised, one on the basis of *Thaxteriola* and *Endosporella*, and then on the basis of *Stigmatomyces Sarcophagae*. *Thaxteriola* and *Endosporella* (Fig. 262, 2 to 4) are two entomogenous imperfect genera which superficially resemble the male plants of the Laboulbeniales and undoubtedly may be regarded as such. If the spores formed by them are spermatia, one must assume that these in some mystical manner reach a distant, still unknown female plant. It is more reasonable to regard them as conidia and their mother plants as imperfects, thus explaining their isolated growth.

The relationships in *Stigmatomyces Sarcophagae* are similar. There we have normally male plants with "antheridia" and female plants with ascogonia. Besides, the same "antheridia" also occur on female plants. It is not feasible to consider the male plants as reduced and their generation as a cause of androgyny, for their antheridia are morphologically and functionally equivalent to those on monoecious plants. It seems much simpler to assume that the supposed antheridia are conidiophores.

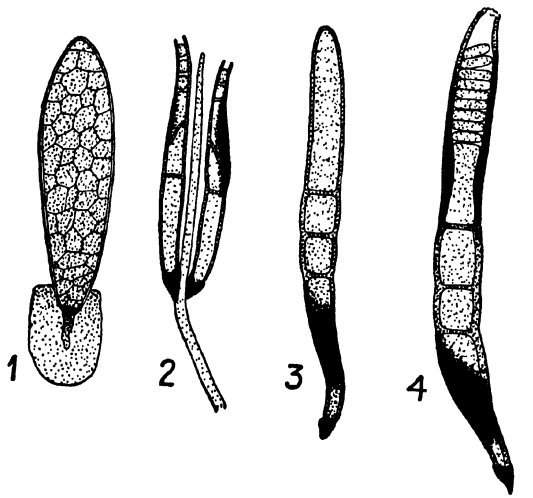


FIG. 262.—1. *Amphoromorpha blattina*. Mature plant on the antenna of a Blattidae. 2. *Thaxteriola nigromarginata*. 3, 4. *Endosporella Diopsidis*. Young and mature individual. (× 600; *after Thaxter*, 1920.)

Thus these conidiophores belong to the same type which we have described for *Thielavia* and *Pyxidiophora*. In all the antheridia for which we at present have no direct parallel in the Ascomycetes, their formation from single cell may always be referred to meristogenous pycnia, such as we have shown in *Teichospora salicina* (Fig. 177). The smallness of all these objects may be connected with the general degeneration of the Laboulbeniales in which occasionally all that remains of the thallus is the two basal cells. If the conidia should prove to be no longer capable of germination, they would be morphologically similar to the microconodia of the Sphaeriales and Phragmobasidiomycetes.

According to this conception, the Laboulbeniales would have a position in the Pyrenomycetes like that of the Uredinales in the Phragmobasidiomycetes. Most would have had a dioecious sexual differentiation; the male individuals bore antheridia such as are still present in the Plectascales; the female bore ascogonia such as we still

know. Besides, both have imperfect forms, as still happens in dioecious Ascomycetes. The perithecia arose in a way such as still occurs in relatives of the Plectascales, the Sphaeriales (*Sordaria* and *Teichospora*) by division of a single mother cell. The male sexual organs, as happened in the Plactascales, Pezizales, etc., degenerated so that in the male individual only the imperfect stage remains. In this manner, the numerous sterile (imperfect) mycelia of the Ascomycetes might be explained simultaneously. They are male mycelia without sexual organs. In compensation for lost gametangial copulation there followed a deuterogamous fertilization of ascogonia by conidia. In the dioecious forms, chiefly, the conidia of the male individual may have served as these secondary spermatia and have apparently secondarily retained some sexual tendencies or affinities. Apparently the conidia of the female individuals can fulfil the sexual function as the example of *Stigmatomyces Sarcophagae* allows one to assume.

Thus in the Laboulbeniales, as in the Pezizales and in the Discomycetous lichens, the function of the conidia as spermatia would be a secondary phenomenon, a consequence of the degeneration of the male sexual organs. Their copulation with trichogynes would be fundamentally the same process as copulation of oidia and hyphae in the Basidiomycetes except that in the Ascomycetes the female organs are recognizable as such, while in the Basidiomycetes they have disappeared like the male sexual organs, so that the sexual act occurs pseudogamously between the hypha and imperfect form.

It is clear that these suggestions do not solve the problem of the phylogenetic derivation of the Laboulbeniales. We were only attempting to show that in case one wishes to maintain the phylogenetic unity of the Ascomycetes, it is possible to regard the Laboulbeniales as degenerate Pyrenomycetes. Many problems await explanation. Thus in the Ascomycetes we know no other group like the Laboulbeniales, which possesses a definite number of ascogenous cells with unlimited capacity for division. At present such cells are known only in the Basidiomycetes. Similarly, the significance of the appendages is still puzzling; the example of the *Corcomyces* where the lower cells of all appendage cells are adapted to conidial formation, tempts one to assume that the appendages were originally conodiophores which, however, like the sporangiosphores of *Chaetostylum Fresenii* and *Chaetocladium Brefeldii*, because of scanty nourishment have ceased conidial formation and have undergone a functional change to become setae.

If, however, one is not inclined to the derivation of the Laboulbeniales and the Pezizales from the Florideae, as was proposed sixty years ago by Sachs and more recently by Vuillemin (1912), B. O. Dodge (1914) and Fink (1915), there still remain as roots of the Ascomycetes two orders, the Oomycetes (Bary's school) and the Zygomycetes (Brefeld's school). The derivation from the Oomycetes is based chiefly on the similarity in manner of formation of eggs and ascospores and on external morphological relationships between copulation tube and trichogyne. The comparison of egg and ascospore presupposes a homologization of oogonia with asci; this is untenable, however, because of the different positions of these organs in the change of nuclear phase. Besides, Wettstein (1921) points out that the Oomycetes known at present have a cellulose membrane but the Ascomycetes, like the Basiomycetes and Zygomycetes, have a chitinous wall.

The above speculations are partially open to criticism on the ground of insufficient knowledge of variation which results from a study of a large series of specimens of a group. Thus, it may be pointed out that the discussion of the transition from endo- to ectoparasitism is of no phylogenetic significance, since this habit has arisen independently in unrelated groups. Biologically, it is an adaptation to the host, haustorial development being usually related to the softness of the body of the insect, and to the nature of the integument. Ordinarily the foot penetrates the integument over a pore canal and the organism is able to get sufficient nourishment from the blood of the

insect through the unthickened portion of the foot, while the hard integument furnishes the necessary support to prevent the fungus being knocked off during the movements of the insect. If the integument is soft, the haustorium may provide additional support as well as nourishment, since it is highly branched and ramifies through the rich, fatty portion of the insect. In part the above series results from the difficulty in technique of carefully dissecting out the rhizoidal portion of the haustorium, hence figures often give an inadequate impression as to the development of the haustorium.

The assumption that the food is not rich is incorrect, since the foot is always bathed by the body juices of the insect, and the cells of the fungus usually contain large numbers of fat globules. As in all other cases where a large amount of reserve energy must be stored in a small space, it is stored as fat. They can hardly be called xerophytic, since their base is always bathed in a suitable supply of water and they spend most of their life in a humid atmosphere. They are well protected, however, against sudden changes in humidity such as might occur if the host temporarily moved into a drier situation. It is very questionable whether this adaptation has influenced their phylogeny.

It is also questionable whether they should be regarded as a degenerating group. It is true that they are small, as an adaptation to a highly specialized environment which has also greatly influenced the development of the thallus in other parasites of living insects, but they have a highly specialized thallus in many forms, usually much more highly differentiated than the individual cells in other groups of fungi.

Without entering the controversy on the derivation of the Ascomycetes from either Florideae or Zygomycetes, certain statements in the argument need correction. It seems just as reasonable to regard the spermatia of *Zodiomyces* which are often sought out by the trichogyne as spermatia as to regard them as conidia which have secondarily been differentiated as spermatia. In many groups spermatial formation ceases soon after fertilization, and a case like *Stigmatomyces Baeri* is an exception rather than the rule, in fact it is not a characteristic of this species. Even in the red algae the formation of spermatia is not closely linked with the presence of a mature trichogyne on a given individual.

While as a rule antheridia may arise from either cell of a germinating ascospore, in some groups it is confined to one cell, as in *Rickia* (the basal). The perithecium usually is developed from the basal cell, but in *Coreomyces* from the terminal.

The condition mentioned in *Amorphomyces Falagriae* is the typical condition in all dioecious forms, although in other respects *Amorphomyces* is an aberrant type. Since the trichogyne is a very evanescent structure, and since the perithecium grows rapidly after fertilization, eventually the antheridia may be far removed from the mouth of the mature perithecium, yet when young, the trichogyne is usually close to the mouth of the antheridium. In these dioecious types, sex differentiation seems absolute. No instances are known where the females produce antheridia or the males perithecia, even in such unusual types as *Dimeromyces adventitiosus*, in which antheridia and perithecia are developed, not only in the normal position from the receptacle, but adventitiously from the ordinarily sterile portions of the male and female individual, as the case may be. Unfortunately these forms have not been studied cytologically.

While Gäumann states that the entomogenous genera of imperfects, like *Thaxteriola* and *Endosporella*, may "undoubtedly be regarded" as male plants of Laboulbeniales, he presents no evidence in support of his statement, and such an interpretation seems incorrect in the light of our knowledge of sex differentiation and the discharge of ascospores in all the dioecious groups of Laboulbeniales.

In the example given of *Stigmatomyces Sarcophagae* to which might be added *Laboulbenia elongata* and others, the plants are normally dioecious, and "male individ-

uals" only result when for some reason the perithecium aborts, and an abnormal multiplication of antheridia sometimes results as a teratological phenomenon. The "female plants" always have antheridia in the usual position.

The simple antheridia seem to have little in common with the conidial forms of *Thielavia* and *Pyxidiophora*, either in appearance or ontogeny, although no cytological studies have been undertaken on either group.

Summary.—The derivation of Ascomycetes from Zygomycetes, which forms the basis of our treatment, is built on the following conceptions. In the Zygomycetous series there are present the beginnings of a threefold development. In the first place, in the privileging of sexual nuclei: all the gametangial nuclei are no longer activated as sexual nuclei or, in any case, do not all take part in the sexual act, but the sexual function is fulfilled by a small portion of them and finally by only one gametangial nucleus (*Endogone*). Secondly, in the Zygomycetes there appears the beginning of a delay in caryogamy which no longer normally takes place in the gametangium, but in outgrowths of it (*Phycomyces*, *Endogone*). And thirdly, the zygospore germinates increasingly by a germ sporangium (*Polyphagus*, *Phycomyces*) rather than a germ tube.

According to the theory presented here, these three tendencies are realized in the lowest Ascomycetes. *Dipodascus* differs from the *Endogone* only in forming a sporangium instead of a zygote as the product of the sexual act. This difference, however, may rest chiefly on biological relationships. In *Dipodascus*, as in *Endogone*, two coenocytic copulation branches enter into open communication. As in *Endogone lactiflua*, however, only one gametangial nucleus from each gametangium participates in each sexual act, so that all other gametangial nuclei are superfluous. While in *Endogone* the supernumerary nuclei soon disintegrate, in *Dipodascus* they are retained longer. Thus between *Endogone* and *Dipodascus* there is a difference like that between the *Pythium–Phytophthora* group and the higher species of *Peronospora* of the Oomycetes. In the latter, the supernumerary peripheral oogonial nuclei persist and are used for secondary vegetative purposes. In *Dipodascus* the supernumerary nuclei are used for accessory structures, apparently in connection with the surplus protoplasm.

This similarity in functional differentiation of gametangial nuclei has led in both groups to similar morphological developments. In the higher Oomycetes, the egg cells were differentiated by free cell formation from the oogonial protoplasm about the sexual nuclei, while the supernumerary nuclei lay outside in the peripheral periplasm. Similarly in *Dipodascus*, the spore portions about the daughter nuclei of the primary ascus nucleus are cut out of the ascus protoplasm by free cell formation while the sexually inactive nuclei remain undivided in the periplasm. If all the nuclei lying in the young ascus were equivalent, as they are in the sporangium of *Polyphagus*, this complication would never have arisen; but the ascus

protoplasm, as in the sporangial protoplasm of *Polyphagus* and the Mucoraceae would have been divided by direct cleavage into the individual spore portions. The nuclei in the young ascus of *Dipodascus* are not equivalent to each other, however, since true ascospore nuclei, *i.e.*, products of the sexual act and meiosis, and ordinary vegetative or sexually inactive gametangial nuclei appear side by side or intermingled. In such a cleavage the vegetative and ascospore nuclei would both enter into the ascospores. This could be avoided only by free cell formation.

According to this conception, free cell formation in the higher Oomycetes and in the ascospores of *Dipodascus* is only a convergence phenomenon, since in coenocytic gametangia, only a selected number of sexual nuclei participate in fertilization, while the others are vegetative and do not enter the new organs (egg cells, ascospores). The ascus of the *Dipodascus* and of the Ascomycetes altogether and the oogonium of the Oomycetes are analogous not homologous organs, as Bary assumed. Whether in both cases the cytological processes are identical to the smallest detail, can be explained only by a closer investigation of *Dipodascus*.

From the *Dipodascus* type a further stabilization of the ascus has occurred since its spore number, corresponding to the number of the tetracyte nuclei, is fixed at eight. The ascus is phylogenetically a germ sporangium become gonotocont, with the correspondingly fixed spore number. Thus the sporangia of the Zygomycetes would have undergone a cleavage, those which normally served further as imperfect forms gradually change to conodiophores as in the *Choanephora–Aspergillus–Penicillium* series; those which functioned as gonotoconts, however, retained their sporangial character at first and only lost it later in the transition from Ascomycetes to Basidiomycetes. In contrast to this morphological stability, biologically the ascus undergoes a manifold functional development which reaches its high point in the discharge organs of the Discomycetes.

In the second place, from the *Dipodascus* type, a development of the female copulation branch (*e.g.*, differentiation into the ascogonium and trichogyne) has occurred while the male copulation branch shows a great constancy and degenerates early. Consequently, in place of the original gametangial copulation, there appear all sorts of deuterogamous processes, the most noteworthy of which is copulation with conidia. The fact that in certain parthenogamous forms the trichogyne is lacking, while in others it has reached a high degree of development, leads one to suppose that in the latter it was made to serve secondary purposes.

In the third place, the retardation of caryogamy which has already caused fertilization to be transferred from the gametangium to ascus continues still further, so that meanwhile the dicaryon divides repeatedly. Consequently the gametangia do not develop directly to asci, but, in a certain sense, vegetatively to dicaryotic hyphae, the ascogenous hyphae,

CHAPTER XXVI

POLYPORALES

The Polyporales include the gymnocarpous stage of the Chiastobasidiomycetes and ascend from simple forms with a hymenium which is spread out over the substrate in an arachnoid layer without definite margins to resupinate crusts, to typical pileate fungi, and finally form the starting point for the angiocarpous line of development which attains its maximum in the stink-horns of the Gasteromycetes.

The hymenophore is always on the outside and, in the simpler forms, is smooth. In the higher groups, it forms anastomosing wrinkles, folds or lamellae, which sometimes have shallow grooves between them, sometimes deep, tubular or elongate cracks or holes. In the highest forms, it is generally divided into pores which have given the scientific name, Polyporales.

The hymenia, in contrast to the Agaricales (except Lactariaceae), are often formed when the young hymenophore is still smooth. With the development of folds and tubes, new and younger elements are always added laterally. Similarly, in a given zone, they develop successively rather than simultaneously, so that old and young basidia are intermingled. In many species with perennial fructifications, in each growing period a new hymenophore is laid down over the old hymenium, so that these are equivalent to annual rings of vascular plants.

In contrast to those of the Cantharellales, the basidia (Fig. 339) are very regular in their structure and generally have four spores. By maturity they become more or less clavate without noticeable elongation, the spindles of all the nuclear divisions lie transversely at the same height near the tip, mostly directly under it (chiastobasidial type). The diploid nucleus divides only twice so that the young basidium is generally quadrinucleate. A third nuclear division appears rarely or not at all; possibly it is removed to the spore whose nuclei generally divide in the young stage. This division, however, is not always completed.

As imperfect forms, oidia are known in many genera, in some also gemmae and typical conidia.

The Polyporales contain over a hundred genera with several thousand species; they include heterogenous types which in their extremes are very characteristic but pass through numerous intermediate forms retrogressively toward ancestral types. Therefore systematic classification cannot be accomplished according to fundamental characters, but only

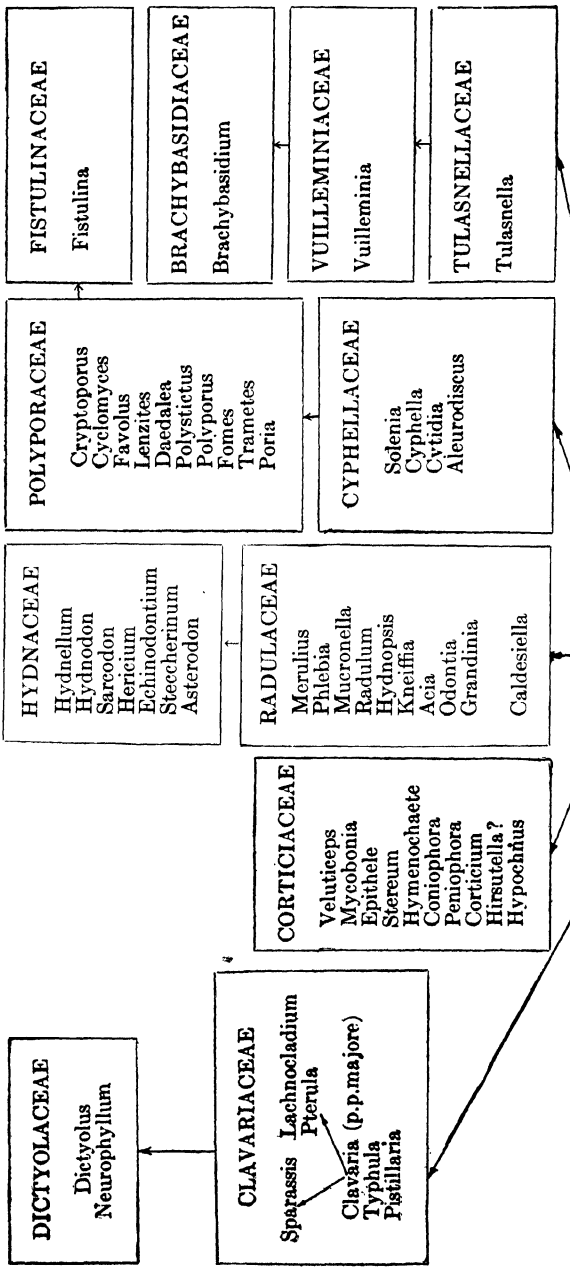


DIAGRAM XXVIII.

according to the end forms of the different series toward which they develop. In this sense, the following ten families, whose characters will be given in the course of the discussion are different. Their probable relationships are given in the scheme on page 430.

Tulasnellaceae.—Perhaps in *Tulasnella* we have an example of the transition from the endogenous spore formation of typical Ascomycetes to the exogenous formation in the Basidiomycetes. The family presents a series with gradual adaptation to parasitism, accompanied by the development of the zeugite to a special storage organ. This development is analogous to that we shall find in the Auriculariales and Uredinales. The highest stage attained seems to be that reached by *Cystobasidium*.

Tulasnella (*Prototremella, Pachysterigma, Muciporus*) is mostly saprophytic on bark or dead wood, occasionally parasitic on leaves

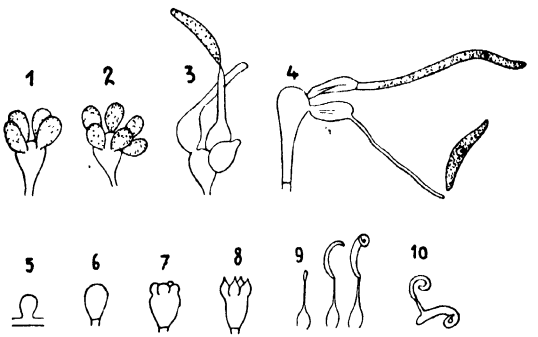


FIG. 273.—*Tulasnella deliquescens*. 1, 2. Basidia with basidiospores. 3, 4. Basidia developing uninucleate conidia (× 355; *after Juel*, 1897.) *Tulasnella helicospora*. 5, 6. Young basidia. 7. Basidium with basidiospores. 8, 9. Development of basidiospores to conidia. 10. Development of conidium to secondary conidium. (*After Raunkiaer*, 1917.)

(*e.g., T. grisea* on *Eichhornia speciosa* in Java and *T. anceps* on *Pteris aquilina* in Europe). On the substrate they form a bloom which may thicken to a smooth corticiaceous crust. In *T. deliquescens* its consistency is slimy; in others, as *T. thelephorea*, the gelatinization of the hyphae is not marked and the consistency is waxy. *T. cystidiophora, T. hyalina* and *T. traumatica* have gloeocystidia in their hymenia and are often segregated as *Gloeotulasnella*. In about half the species the spores are nearly spherical while in the other half the spores are long fusiform, and sometimes curved. The hyphae are binucleate and much branched; in *T. deliquescens*, there are no clamps and the basidia, which are terminal on the ultimate branches, are irregularly placed and imbedded in the gel, while in *T. thelephorea*, clamps are abundant, the basidia are more fasciculately arranged and form a simple layer on the young crust which does not show the regular parallel structure of a typical hymenium.

The basidium is pyriform and is cut off by a septum (Fig. 274, 3). The nucleus goes through two stages of division. At the tip, seldom

laterally, arise four, occasionally five or six, protuberances which become ellipsoidal, sessile spores (Fig 273, 1 and 2). In damp weather they germinate while on the basidium without being abjointed, and each forms a short germ tube (Figs. 273, 3 and 4; 274, 8 and 9) which may branch and swell terminally to a conidium, slightly curved and pointed at the end. The conidia abjoint and germinate immediately, in *T. helicospora* by further sprouting. In *T. deliquescens*, the basidiospore, the germ tube and conidia are uninucleate; in *T. thelephorea*, the basidial nucleus, immediately after its entrance into the spore, passes through a third division (Fig. 274, 7); hence its mycelium is wholly binucleate (Brefeld, 1889; Juel, 1897, 1898, 1915; Raunkiaer, 1918).

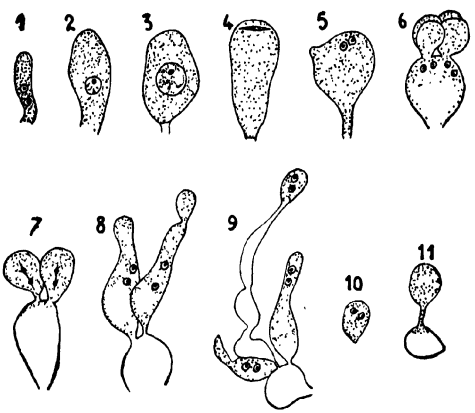


FIG. 274.—*Tulasnella thelephorea*. 1 to 5. Development of basidia. 6. Basidium with four basidiospores. 7. Caryogamy in the basidiospores. 8, 9. Germination of basidiospores with conidium. (1 to 7, 10, 11 × 535; 8, 9 × 355; *after Juel*, 1897.)

The above interpretation of the reproductive organs follows that of Juel. Patouillard (1888) regarded the "basidia" of the above description as probasidia, the "spores" as basidia, the "germ tubes" as sterigmata and the "conidia" as basidiospores. The spores were regarded as the four separate cells of the cruciate basidium and hence related to the Tremellaceae. Neuhoff (1924) revives this conception, replacing the probasidium by the term hypobasidium and the cruciate basidium by epibasidium. Hoehnel and Litschauer report that there is a complete series of transitions between the slender sterigmata of the Corticiaceae and the "spores" of *Tulasnella* and consequently regard the sessile spores, which are never abjointed, as swollen sterigmata and the conidia as true basidiospores. Raunkiaer (1918) and Burt (1919) agree with this conception and the latter places *Tulasnella* in the Thelephoraceae (*sensu latiore*) near *Aleurodiscus*, where the sterigmata are often swollen at the base.

If Juel's interpretation is correct, *Tulasnella* with its sessile basidiospores germinating *in situ* is unique in the Basidiomycetes, and does not seem closely related to any other group. If the basidium is conceived as developing from an ascus by gradual exogenous spore production, perhaps *Tulasnella* represents a transitional stage where the spore mass, without secreting a wall about itself, is pushing out of the gonotocont without having reached the stage of a separate entity before it germinates. The very primitive (or reduced) structure of the thallus points in this direction. On the other hand, such a conception would indicate that it had not yet reached a suitable mechanism for spore discharge, having lost that of the ascus without having attained that of the basidiospore. A study of the mechanism of spore discharge, as proposed by Buller, to see whether the "conidium" of Juel's interpretation is discharged as a conidium or a basidiospore, would do much to clarify the situation.

Vuilleminiaceae.—The only species of this family, *Vulleminia comedens* (*Corticium comedens*) (Maire, 1902), grows on dead oak twigs where

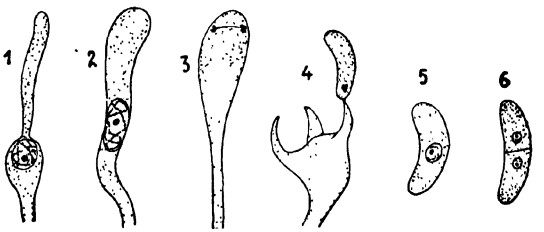


FIG. 275.—*Vuilleminia comedens*. 1. Germinating zeugite. 2, 3. Young basidia. 4 Mature basidium. 5, 6. Germinating basidiospores. (× 500; *after Maire*,190 2.)

it separates the bark from the wood and forms gelatinous corticiaceous crusts 0.1 to 0.2 mm. thick. The basidia are formed in the interior of the hyphal tissue and emerge singly at the surface. The hyphae are binucleate, the terminal cell of a branch swells, the dicaryon fuses and the zeugite puts forth a slender basidium (Fig. 275, 1) which reaches the open air, broadens considerably at the tip and, after a second nuclear division with transverse spindles, forms four uninucleate basidiospores, in which the nuclei divide and sooner or later a septum is laid down (Fig. 275, 6).

Brachybasidiaceae.—The only species of this family, *Brachybasidium Pinangae*, parasitic on the pinang palm in the rain forest of West Java, bears the hymenium erumpent from the stomata as a small granule on the under side of the leaf. As in *Vuilleminia*, the terminal cells of the hyphae swell to form storage cells, which in this species are united into a small sorus and possess a firm wall (Fig. 276). From time to time such a probasidium swells, protrudes its tip above the sorus and becomes a basidium which (in contrast to *Vuilleminia*) is not swollen at the tip, but bears two sterigmata. As in *Vuilleminia*, the basidia are chiastobasidia.

Brachybasidium is very interesting from the viewpoint of comparative morphology; for there can be no doubt that this thick-walled probasidium affords protection and makes it possible for the basidium to await favorable conditions for germination. In this sense, it is comparable to the sclerobasidia of the Phragmobasidiomycetes. The chiastobasidial Autobasidiomycetes have attained the same degree of development in this family as the stichobasidial Phragmobasidiomycetes in the Septobasidiaceae, and the lepto-forms of the Uredinales.

Corticiaceae.—This family includes the simplest forms of the Polyporales; they show beginnings of the various directions of development and form thereby, as is shown in the scheme on page 430, the key to the

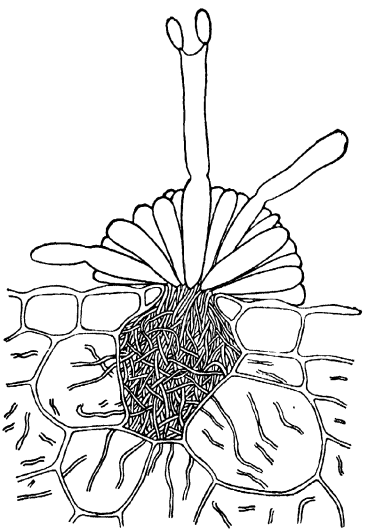


FIG. 276.—*Brachybasidium Pinangae.* Section of zeugite sorus with three germinating zeugites. (× 390; *after Gaumann*, 1922.)

whole order. Their representatives are mostly saprophytes on earth, wood or dead parts of plants. Their basidia are generally four, more seldom two, or six to eight spored. Usually their spores are hyaline and smooth, rarely, as in *Hypochnus* (*Tomentella*), rough and brown or yellow.

According to the structure of their fructifications, they may be divided into three intergrading stages of development. The forms of the lowest stage, as *Tulasnella* of the Tulasnelaceae, *Helicobasidium* of the Auriculariales and *Sebacina* of the Tremellales, spread out on the substrate in an arachnoid covering; the basidia rise, like free conidiophores, at unequal heights on the same hyphae, singly or in candelabra (Fig. 265, 1); thus there are formed no, or only diffuse, fructifications and hymenia. In the second stage, the hyphae intertwine to homogeneous, leathery or

fleshy cushions, as *Platygloea* in the Auriculariales and *Sebacina* in the Tremellales, and may be designated as true crustose fructifications. Their basidia rise to the same height, and crowd together as an even hymenium which is broken only by cystidia. In the third stage, the hyphal cushions increase to bracket or even centrally stipitate fructifications. The context loses its homogeneous structure and is differentiated into a sclerotic rind and solid middle layer. Thereby, they become very resistant to external influences; while the hyphal tissue of the first two groups appears in damp weather and in drought collapses and becomes invisible, or is entirely ephemeral, the fructifications of this third group survive climatic variations and at times attain great age.

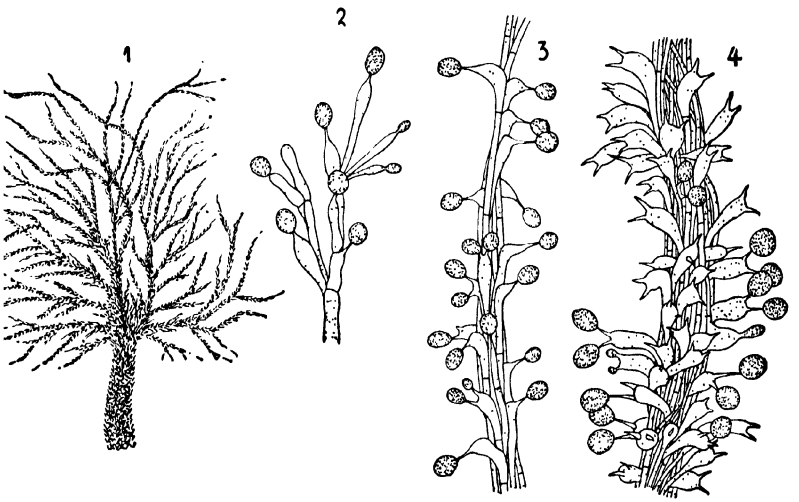


FIG. 277.—*Hirsutella varians*. 1. Habit. 2. Conidia. 3. Apparently a transitional stage from conidia to one- and two-spored basidia. 4. Basidia. (1 × 16; 2, 3 × 390; 4 × 780; *after Boulanger*, 1893.)

In the first group are many species of *Exobasidium* (see p. 413), *Hypochnus*, *Hirsutella* and a small group of semiparasitic species of *Corticium*, while the remainder of *Corticium* belongs rather to the second group. In *Hypochnus* and *Corticium*, the basidia are borne on a resupinate hyphal tissue, in *Hirsutella*, on coremia. All three groups form very loose, flocculent or mealy, white or bright-colored wefts which in the higher species thicken to a fibrous tissue. At maturity, the hyphae branch and form basidia on their ends. In many species, the subterminal cell grows laterally to a new basidium which pushes the old one aside and later is itself pushed aside by the younger ones. By the continuous formation of new basidia and groups of basidia, the basidial layer becomes thicker and thicker and in some species gradually develops to a more or less continuous hymenium.

In some species, the formation of a basidium is preceded by a luxuriant conidial formation. In *Hypochnus isabellinus* (*Tomentella flava*) (Brefeld, 1889), there appear in certain parts of the hyphae, numerous lateral branches which, throughout their whole length, cut off a large mass of red-brown, echinulate spores on short sterigmata (Fig. 278). Before the connection of these spores and *Hypochnus* was known, they were called *Botrytis argillacea*. In *Hirsutella varians* (*Matruchotia varians*) the hyaline conidia are cut off over the whole expanse of the mycelium. With the exhaustion of nutrient solution, the hyphae collect in coremia which gradually proceed to the formation of "basidia" (Fig. 277). These appear to be connected with conidiophores by a continuous series of intermediate forms (Boulanger, 1893).

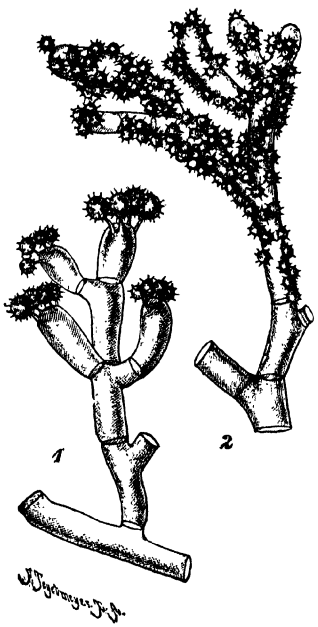


FIG. 278.—*Hypochnus isabellinus*. 1. Hypha with basidium. 2. Portion of a conidiophore. (×350; *after Brefeld*, 1899.)

The name *Corticium* from cortex, bark, indicates the fructifications of all these genera are resupinate, they are directly connected to the hyphal tissue of *Hypochnus* and in these simple forms are thin, membranous, at times arachnoid, while in the higher forms fleshy or leathery, and generally attached to the substrate over the whole expanse; thus the cosmopolitan *Corticium vagum* (*C. botryosum*, *Rhizoctonia Solani*), the cause of *Rhizoctonia* disease of potato and other vegetables, often subterranean, sheathing the roots or stems, is hypochnoid. *C. salmonicolor* (*C. javanicum*), which causes serious necrosis of bark and twigs of tea, coffee, cacao and cinchona in the tropics, has more luxuriant coverings and a continuous hymenium. In *C. Koleroga* (*Pellicularia Koleroga*) which causes a thread blight of coffee, the basidia are borne directly on hyphae in mycelial strands covering the under surface of the leaves and extending down the twigs. *C. Stevensii* (*Hypochnus ochroleucus*), a thread blight of apple, pear and quince in Brazil and the southern United States, differs in having chestnut-brown sclerotia 3 to 4 mm. in diameter and slightly more compact masses of basidia-bearing hyphae.

In genera of the second stage of development, systematic classification is founded on all sorts of artificial characters; thus one places in *Corticium* (spores hyaline, thus distinct from *Hypochnus* and *Coniophora*) chiefly those forms whose hymenia consist exclusively of basidia; in *Peniophora*

(spores hyaline) those with cystidia and gloeocystidia (Fig. 279); in *Epithele* (Fig. 280), *Veluticeps* and *Mycobonia* those with curious sterile hyphal pegs, *etc.*, springing from the subhymenial tissue and projecting above the hymenium. In short the system only gives first aid and hence is variously treated by different authors. Cytologically, of all these forms only *Corticium lacteum*, *C. bombycinum*, *Peniophora Sambuci* and *Hymenochaete tenuis* (*Hypochnus subtilis* of Harper) (Maire, 1902; Harper, 1902; Kniep, 1913) have been studied.

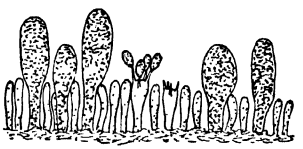


FIG. 279.—*Gloeocystidium clavuligerum.* Section of hymenium showing basidia and gloeocystidia. (× 385; *after Hoehnel and Litschauer*, 1906.)

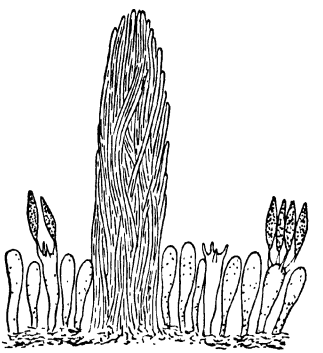


FIG. 280.—*Epithele Typhae.* Section of hymenium showing a peg of hyphae. (× 255; *after Hoehnel and Litschauer*, 1906.)

Coniophora cerebella develops very thick (often 0.5 mm.) crusts, at first fleshy and membranous, later dry and brittle. This species is as important a cause of dry rot of coniferous timber in the United States as *Merulius lacrymans* in Europe. *Corticium centrifugum*, *C. Stevensii* and *C. radiosum* (*C. alutaceum*) form bulbils (sclerotia) which when dried retain their ability to germinate for several years and under favorable conditions develop to mycelia.

In *Peniophora candida* (*P. Aegerita* and *Kneiffia Aegerita*) these bulbils

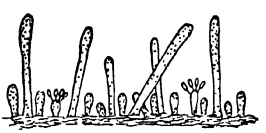


FIG. 281.—*Peniophora chordalis*, showing basidia and cystidia. (× 265; *after Hoehnel and Litschauer*, 1906.)

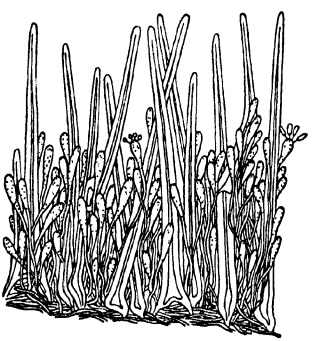


FIG. 282.—*Peniophora chaetophora.* (× 200; *after Hoehnel and Litschauer*, 1907.)

consist of single much-branched hyphae whose branches are much intertwined; generally, in the young stages, the peripheral hyphal ends swell terminally and each cuts off one, seldom several, thin-walled conidia. These bulbils often appear in such large quantities that the hymenium is not formed; they loosen from the hyphal cushion and undoubtedly play

an important role in the dissemination of the fungus. They are probably homologous to the hymenial bulbils of *Rhacophyllus lilacinus*. In other species, *e.g.*, *Peniophora chordalis*, the cystidia stand far above the hymenium (Fig. 281). In *P. chaetophora*, they are branched and project above the hymenium in the form of setae, serving as a support for the outer, loose hymenium which creeps up them (Fig. 282). When young, they are binucleate; after the degeneration of the nucleus they contain only a clear content. In many species they are covered with calcium oxalate.

As imperfect forms, conidia have been demonstrated in *Corticium* and *Peniphora* (*Kneiffia*) (Lyman, 1907; Hoehnel and Litschauer, 1906). In *C. radiosum*, they arise (occasionally on the clamp-bearing mycelium itself) on short, characteristically branched conidiophores and are bacilliform or oidia like. In *C. roseopallens*, they are usually cut off in tufts on short branches and are slightly curved. In *C. effuscatum*, they arise on the hyphae or on capitate swollen conidiophores, and are spherical, these capitate conidiophores correspond to the *Oedocephalum* type in the imperfects and are again met among the Polyporaceae in *Fomes* (Fig. 288). In *Peniophora coronilla* the conidia are cut off in groups of eight on short sterigmata and appear, externally, very similar to the basidiospores. In *Corticium effuscatum* and *C. subgiganteum* are formed thick-walled gemmae. In the latter species they appear subterminally on palisade hyphae and may then be regarded as a highly specialized gemma hymenium. This gemma fructification was earlier considered as a separate species. Similarly, the gemmae of *Peniophora Habgallae* were described as *Artocreas poroniaeforme* and *Michenera Artocreas* (Petch, 1926). *Corticium niveocremeum* has six-spored basidia of which two spores abort, since only four nuclei are formed in the basidium, and the four fertile spores are uninucleate (Kuehner, 1926).

Hymenochaete belongs to the third stage of development. As the name indicates, this genus is characterized by the presence of elongate, conical, brown setae, which blacken promptly with a solution of KOH. The setae are arranged in layers often suggesting annual rings (Burt, 1918). *Hymenochaete* is predominantly tropical with a rapid decrease of number of species in the temperate regions. In these, the Corticiaceae reach the highest stage of development. Their fructifications are leathery, woody or corky. *Stereum* also begins with simple resupinate forms, gradually raises its edges from the substrate, and extends horizontally, becoming laterally attached brackets and simple stipitate fructifications. *S. hirsutum* and *S. fasciatum* are instructive examples of the dependence of the form of the fructification on its position on the substrate. In horizontal substrates the fructifications are resupinate with up-turned margins, radial in structure with the hymenium downwards. On vertical substrates they extend horizontally

from the substrate, turn the hymenium downwards and are notably dorsiventral (Goebel, 1902; Burt, 1918). They may even become stipitate if growing on the upper surface of a log. They are generally gregarious and imbricate on trees, causing an asphyxiation of the wood.

Another species, *Stereum purpureum* on fruit trees, raises the epidermis of the leaves from the palisade layers in vesicles, which fill with air, obscuring the chlorophyll, hence the name "silver-leaf disease"

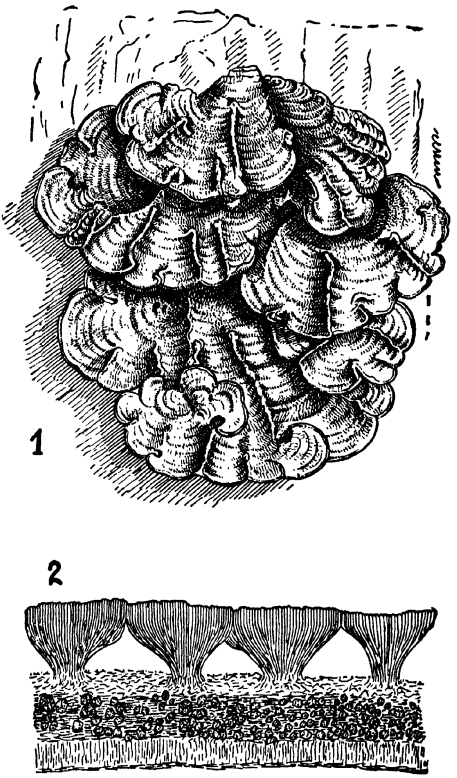


FIG. 283.—*Cora pavonia*. 1. Thalli on tree trunk. 2. Section of fruiting thallus. The dark, spherical structures are gonidia. The reproductive layer is formed of papillae. (1 × ⅔; 2 × 33; *after Johow*, 1884.)

(Brooks, 1911, 1913). A third species, *S. frustulosum* (*Thelephora perdrix*), causes the partridge-wood disease of oak.

Hymenochaete noxia, an extremely polymorphous and plurivorous fungus, is a root parasite in the tropics seriously damaging *Hevea*, *Theobroma Cacao*, *Thea* and dadap.

Of special biological interest is the tropical *Stereum* which forms the lichen *Cora pavonia* with the alga *Chroococcus* as gonidia (Fig. 283, 1).

This grows on shrubs and tree trunks, on rocks and banks of earth forming blue-green brackets, with lighter margins. At the beginning of fructification, it develops on the lower side numerous spreading hyphal fascicles, whose branches terminate in four-spored basidia (Fig. 283, 2). The fungus appears in Nature without the alga and forms brackets; in living with the alga, it attains much larger dimensions, and is able to thrive in places where it would not grow alone, *e.g.*, in the forest crown. With another alga, *Scytonema*, it forms another lichen which is placed in *Dichonema* (*Dictyonema*) in systematic literature (Fig. 284, 1). Under certain conditions in this association, not the fungal hyphae, but the alga determines the form of the lichen, so that this lichen is modified to

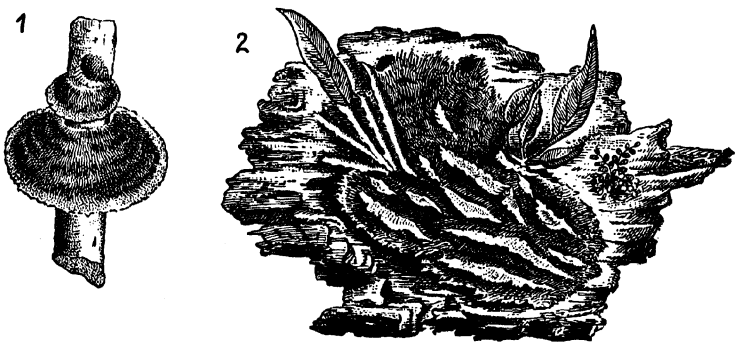


FIG. 284.—*Cora pavonia*. 1. *Dichonema sericeum* form; thallus on twig. 2. *Laudatea caespitosa* form; portion of bark and leaves covered with lichen thallus which bears parallel white hymenia. (× ⅔; *after Johow*, 1884.)

a special *Laudatea* form (Johow, 1884, Möller, 1893). The lichens, as those here, in which the fungus component is a member of the Basidiomycetes, are classed together as Hymenolichenes.

Cyphellaceae.—This family connects directly to the Corticiaceae, especially to the *Corticium* stage. By a strongly hyponastic growth, the fructification develops to a pezizoid cup which contains the hymenium in the interior. Some of the genera are distinguished by a gelatinization of the hyphal membranes.

In the simpler genera, as in *Aleurodiscus* (fructifications waxy, leathery or fleshy) and *Cytidia* (fructifications gelatinous), the fructifications are resupinate crusts in youth. During the course of development the edges are reflexed and the fructification becomes patelliform (Stork, 1920). In *Aleurodiscus*, the hymenia contain peculiar paraphysoid structures; these are thin-walled and smooth, swollen toward the top, and moniform (pseudophyses, Fig. 285, 1); or they may be thin- or thick-walled and covered throughout or in spots with crowded, gener-

ally branched, spines of variable length (dendrophyses Fig. 285, 2). Perhaps they are to be regarded as organs of protection. In addition, gloecystidia have been found in some forms.

In the higher genera, as in *Cyphella* (fructifications membranous), *Cytidia* (*Auriculariopsis*) (fructifications gelatinous), the fructifications are raised from the central point of attachment by a compressed, short stipe; they then assume an infundibuliform or cup shape, whose inner side is corrugated and bears the hymenium.

In *Solenia*, finally, the hyponastic growth begins very early and causes elongate, cylindrical fructifications which are mostly joined gregariously in membranous colonies. Their edges often bend together and enclose the hymenium during drought.

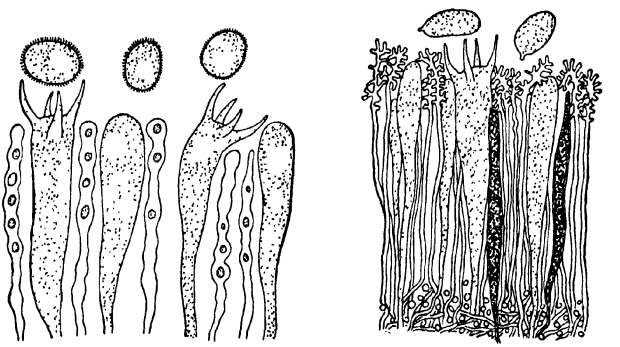


FIG. 285.—*Aleurodiscus amorphus*. 1. Section of hymenium with basidia and pseudophyses. 2. *Aleurodiscus sparsus*. Section of an apical portion of fructification with basidia, dark gloeocystidia and denticulate dendrophyses. (× 335; *after Hoehnel and Litschauer*, 1907.)

Clavariaceae.—While the stichobasidial line discussed in the Cantharellales contains a few representatives of this family, the main group of several hundred forms is probably predominantly chiastobasidial and hence should be discussed under the Polyporales. The simpler genera, *Pistillaria* (two-spored basidia) and *Typhula* (four-spored basidia), develop clavate fructifications from sclerotia and are entirely covered with a hymenium. In a few species of *Typhula*, the hymenium is limited to the tops of the clubs. *T. variabilis* on dry stems and humus and *T. Betae*, on decaying roots of sugar and other beets, winter over with small sclerotia, each consisting of a light core and a dark rind which is cutinized on the outside. The sclerotia germinate in spring to a luxuriant mycelium whose hyphae, in *T. variabilis*, bear an immense number of elongate oidia on short branches (Brefeld, 1887). The hyphae intertwine to thick bundles which swell clavately and proceed to form hymenia. Kuehner (1926) figures typical transverse spindles in the basidial nucleus of *Typhula candida*. In other genera, the fructifica-

tions are mostly strongly branched, as in *Clavaria* (fructifications fleshy) and *Pterula* and *Lachnocladium* (fructifications cartilaginous or horny). Simple undifferentiated forms are also found, however, as in *Clavaria*, section *Holocoryne* (fructifications single, *e.g.*, *C. pistillaris*) and section *Syncoryne* (fructifications connivent at the base, *e.g.*, *C. fragilis*). More important economically are members of the third section, *Ramaria*, with coralloid, branched fructifications, of which many species are used for food. Many of the larger species, as *C. aurea*, *C. amethystina* and *C. formosa*, develop from large, compact, spherical masses of mycelium which may live for more than one year (Weir, 1917).

In *Sparassis*, the branches are flattened instead of terete and often crisped. The fructifications of *S. crispa* (*S. ramosa*) attain a cross-section of half a meter and are prized as food. *S. radicata* causes a yellow root rot of fir (*Pseudotsuga taxifolia*), spruce (*Picea Engelmanni*) and pine (*Pinus monticola*). The fructifications, as those of *S. spathulata*, are thinner than in *S. crispa*. The perennial rooting base usually is attached to the deeper lateral roots of the host and may become 30 to 50 cm. long. The peripheral hyphae in the soil are modified into a hard, resinous encrusting layer. The mycelium at the base of the stalk cements the soil particles into a stony body, often of very large dimensions. The central cylinder is composed of a compact cellular tissue of longitudinal hyphae which become looser above. The mycelium lives in the bast until the root is killed, when its rhizomorphs invade and completely destroy the sapwood. The heartwood is attacked in spots. Apparently the decay never extends above the level of the soil (Weir, 1917).

Dictyolaceae.—This family corresponds to the Cantharellaceae in the stichobasidial group (p. 533) and consists of species which, on account of their chiastobasidia, have been removed from that family. *Neurophyllum* corresponds to the stichobasidial *Craterellus*, *Dictyolus* to *Cantharellus*. The family is apparently connected to the Clavariaceae and merges with it. *Neurophyllum pistillaris* (*Craterellus pistillaris*) is difficult to distinguish from a specimen of *Clavaria pistillaris* with a wrinkled hymenium. *Dictyolus bryophilus* and *D. glaucus* were shown by Maire (1902) to belong to the chiastobasidial group. In *Dictyolus* ? *umbonatus* (*Cantharellus umbonatus*) because of the loose character of the hymenium one may see the tufted arrangement of basidia which is characteristic for primitive genera. Such an arrangement is common in the lower Corticiaceae (Juel, 1916). Only *Neurophyllum clavatum* (*Craterellus clavatus*) is used for food.

Radulaceae.—As understood here, this family includes most of the species placed in the Hydnaceae by the earlier writers. The family is distinguished from the Corticiaceae by the presence of spines or reticulations on the lower surface of the fructification, covered by a hymenium. The family includes all developmental stages from resupinate crusts to

highly developed pileate forms similar to the higher Polyporaceae and Agaricaceae. The ontogeny has not yet been studied. *Irpex* with flattened teeth and *Hydnochaete*, a segregate from *Irpex* with setae in the hymenium, have many points in common with *Polystictus*, and have frequently been considered genera of the Polyporaceae.

In the resupinate stage, the simplest form, *Caldesiella*, corresponding to *Hypochnus* of the Corticiaceae, is of loose, floccose texture with rough, colored spores and conical teeth with fimbriate tips. Corresponding to *Corticium*, *Grandinia* has small obtuse spines covered with a hymenium, while in *Acia* the spines are conical. In *Grandinia crustosa* (*Odontia crustosa*) bulbils like those reported for the Corticiceae, were observed by Hotson (1912). *Acia omnivora* (*Hydnum omnivorum*) has been reported by Shear (1925) as the probable perfect stage of *Phymatrotrichum omnivorum* (*Ozonium omnivorum*) the Texas root rot of cotton. *Kneiffia* is characterized by its gelatinous consistency and its sterile hyphal pegs which tower above the hymenium, as in *Epithele*.

In *Odontia*, *Hydnopsis* and *Radulum* the projections of the hymenophore are more highly developed. In *Odontia* (spores white) and *Hydnopsis* (spores colored) the spines are sterile at the tip and cystidia are present in the hymenium; in *Radulum* the spines are blunt knobs often confluent and scattered irregularly over the fructifications. In *Mucronella* the crust is fugacious and the spines are several millimeters long, appearing deceptively like independent fructifications.

In *Phlebia* the hymenophore is divided by uneven wrinkles which are partly irregular and partly arranged in regular folds or ribs. In many species, *e.g.*, *P. merismoides* which forms orange-yellow or flesh-colored crusts on fallen cherry, the hyphae break up into large masses of ellipsoid oidia which develop in nutrient solutions to mycelia (Brefeld, 1889).

In *Merulius*, the end member of this developmental series, the reticulations are more highly developed and often suggest the pores of the Polyporaceae, but the ontogeny is fundamentally different (Burt, 1917). In *Merulius* the fertile hymenium is at first plane; by further growth, the surface is thrown into folds and becomes porose but the hymenium continues to cover the edges of the pores. In *Poria* of the Polyporaceae, the formation of pores precedes the development of the hymenium. Later a hymenium develops in each pore, as in *Porothelium*, but these hymenia are not continuous over the edges of the dissepiments.

The lower forms are floccose and resupinate, as *M. pinastri*, with spines in the corners of the reticulations so that it was earlier included among the resupinate species of the Friesian *Hydnum*. *Merulius lacrymans* (*Gyrophana lacrymans*, *M. domesticus*), so called because its mycelium is guttiferous in moist situations, is of great economic importance in Europe as a dry rot of timber, although rare in America. Its

rhizomorphs become several millimeters thick, terete, white, tough and flexible when young, gray to black and brittle in age. They consist of a ground tissue of thin-walled vegetative hyphae in which are imbedded a number of functionally specialized hyphae (fibrous, vascular, etc., Fig. 268). These enable the fungus to penetrate unfavorable regions, such as cracks in the walls, and thus reach fresh uninfected wood to continue

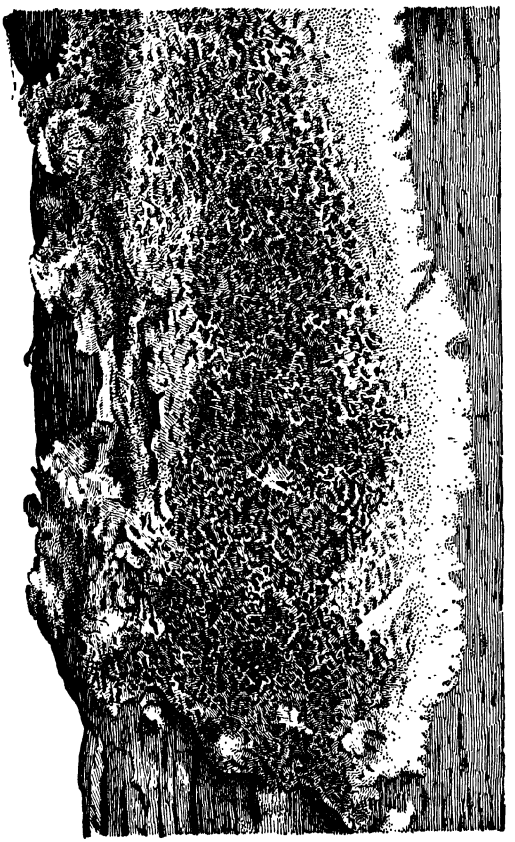


FIG. 286.—*Merulius lacrymans*. Fructifications on rotting beam. (Natural size; *after Falck*, 1912.)

their growth. Upon lack of nourishment, the protoplasm contracts into short sections, surrounds itself with a thick wall and produces gemmae.

The next stage is reached by the reflexed forms, such as *M. tremellosus* which has a broad gelatinous subhymenial layer. The highest stage is reached in the dimidiate forms, which in *M. rubellus* form groups of

imbricated, tomentose, coral-pink fructifications on hard woods, often accompanied by *Stereum fasciatum* in the Mississippi valley.

Hydnaceae.—The pileate genera have an ascending series, as in Corticiaceae and Polyporaceae. In the epixylous genera we have a number of forms corresponding to genera of the higher Corticiaceae: *e.g.*, *Asterodon* with stellate setae in the hymenium corresponding to *Asterostroma*, *Steccherinum*, leathery with hyaline spores, as in *Stereum*, while the perennial woody *Echinodontium* resembles *Fomes* of the Polyporaceae so much that it was originally described in the latter genus. *E. tinctorium* was formerly used extensively as a dye and war paint by the North American Indian. The tuberculiform, branched masses of *Hericium* have long been known as wound parasites and saprophytes, *e.g.*, *H. coralloides* and *H. caput-ursi*.

Finally, in the higher terrestrial genera they have reached the same height of development attained by the fleshy Polyporaceae. *Sarcodon* (spores colored, tuberculate) and *Hydnodon* (spores white, echinulate) suggest fleshy species of *Polyporus* while *Hydnellum* (spores colored, tuberculate) and *Phellodon* (spores white, echinulate) suggest *Polystictus*.

Polyporaceae.—This family in the narrower sense is connected to the *Epithele* group of the Corticiaceae, to *Odontia* of the Radulaceae and perhaps more directly to *Solenia* of the Cyphellaceae. The fructifications in the simpler forms, as in the Radulaceae, develop resupinate crusts or brackets, while the higher forms develop laterally or centrally stipitate pilei. In many species they are tough and perennial. In this case they form a new layer of tubes over the surface of the old ones, either with or without a layer of context separating the layers of tubes. These growth zones resemble annual rings and like them may be used to determine the age of the fructification. The hymenium lines the tubes but their edges are always sterile, in contrast to those of *Merulius* in the Radulaceae.

The family includes several thousand species which merge into each other without sharp limits, hence they have so far escaped satisfactory systematic treatment. They have been classified mainly by macroscopic characters, into a few rather large genera which have been differently defined by various authors. In many groups, microscopic characters which are reasonably constant are available (Overholts, 1915) but have been little used.

The family may be divided into two large groups on the basis of their pores. In the first, the tubes are circular or hexagonal in cross-section while in the second the tubes are labyrinthiform (daedaloid) in cross-section. Except in *Trametes*, in the first group the context (substance of the pileus) is distinct from the trama, usually of a different color.

Poria includes all the strictly resupinate forms with fleshy, leathery or woody crusts on decaying wood. In *Poria vaporaria*, a cause of

timber decay, Brefeld (1889) reported that the hyphae first form a felt with groups of basidia which gradually become more numerous and form compact hymenia. Later, portions of the hymenophore grow rapidly, separating the hymenium into circular discrete areas. The growing edges remain sterile, although the hymenium continues to form on the walls of the developing tubes. On the other hand, Burt (1917) states that he has never found basidia in *Poria* until the pores are fully formed. The difference in many cases is dependent on subjective measurements, particularly of herbarium material.

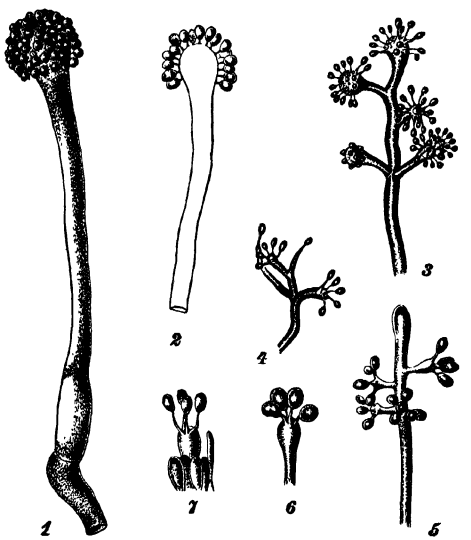


FIG. 287.—*Fomes annosus*. 1. Exterior of normal conidiophore. 2. Section of same. 3 to 5. Small branched conidiophores with heads of few spores in 5, partially reduced to four. 6. Single, basidium-like conidiophore heads with four spores each. 7. Four-spored basidia surrounded by paraphyses. (1 to 6 × 300; 7 × 350; *after Brefeld*, 1899.)

Fomes annosus (*Trametes radiciperda*) is very destructive to pine. The hyphae penetrate the roots, mount the trunk and cause there a red rot of the wood. Fructifications arise at the roots and are mainly resupinate. Every year is formed a new layer of pores which largely covers the older layer like a membrane. There have been reported (Brefeld, 1889) conidia similar to those of *Pustularia vesiculosa* and *Corticium effuscatum* (Fig. 287). The hyphal ends swell to knobs and cut off numerous hyaline conidia on very fine sterigmata of variable length. These conidia can develop to new mycelia while still sessile on the heads. In exceptional cases, there occur little heads with few spores, which are then similar to four-spored basidia and were considered by Brefeld as the

ancestral form of basidia. In good nourishment the conidiophores branch and form coremia.

Some species are used as food, *e.g.*, *Polyporus confluens*, *P. frondosus*, *P. pes-caprae* and *P. sulphureus;* earlier, others were used as medicines (*Fomes officinalis* from its quinine taste); others found technical uses, as *P. betulinus* in the manufacture of charcoal crayons. Still others cause disease of fruit and forest trees and destroy timber, as *Fomes igniarius*, *F. fomentarius*, from whose fructifications tinder was formerly made, *Polyporus squamosus* and *P. sulphureus* and, on old gooseberries and currants, *Fomes Ribis*.

The fructifications of *Fomes igniarius* grow to as much as eighty years old forming a new layer each year. A few species of *Polyporus* form sclerotia up to the size of a human head, as *P. Tuberaster* (E. Fischer, 1891) in the north temperate zone, *P. Berkeleyi*, *P. umbellatus* and *P. frondosus* in the United States, *P. sacer* and *P. Goetzii* in Africa, *P. Sapurema* in Brazil, *P. rhinocerotis* in the Malay region and *P. basilapidiodes* and *P. Mylittae* in Australia. Those of *P. Mylittae* attain a weight of 15 kg. and earlier were eaten by the natives in Australia and called native bread.

The species of *Polystictus*, which number almost a thousand, are saprophytes on wood. *P. versicolor* often attacks fruit trees as a wound parasite. *P. pargamenus* causes decay of a large number of woods.



FIG. 288.—*Trametes* species on wood. Lower view of bracket fructifications showing *Daedalea*-like elevations of hymenophore. (Natural size; *after Falck*, 1909.)

Trametes, as its character is not always recognizable, has been divided by many authors among the above three genera and *Daedalea* (Fig. 288). *Trametes Pini* causes great damage to pines by a red rot of wood. Under certain conditions of nourishment, their hyphae (as in most other Polyporaceae) fall apart into oidia.

Hyaline, pyriform or oval conidia have been noted in *Cryptoporus volvatus* (Zeller, 1915). The hymenium develops on the roof of a large central cavity opened in the interior of a spherical fructification, laterally attached to the substrate. Gradually the portion below the hymenium ceases to grow, the hyphae are stretched into a thinner layer and a small central opening is formed in the veil ("volva"). The spores are shed upon the upper side of the veil, whence they are dispersed by clinging to the legs of insects which crawl over it. The development is therefore hemiangiocarpous, the only case known in the Polyporales and the only group in this order which depends on insects for spore dissemination.

The second group of the Polyporaceae with labyrinthiform pores, shares the fate of the first group in its systematic disorder. Here only three genera will be discussed, *Daedalea*, *Lenzites* and *Favolus*. In the two former, the fructifications are woody, leathery or corky, in the latter

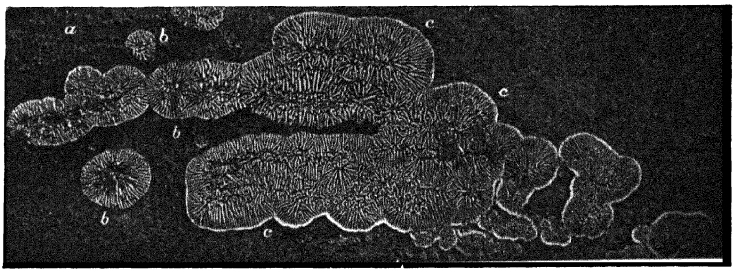


FIG. 289.—*Lenzites abietina*. Resupinate fructification. At *a*, lie numerous denticulate hymenial fundaments, at *b*, somewhat older radiating fructifications, at *c*, irregularly assembled fructifications with common growth zones. (× $\frac{3}{5}$; *after Falck*, 1909.)

more or less fleshy; in all three they are perennial, rarely resupinate, usually brackets. In *Daedalea* the folds are labyrinthiform, seldom almost lamelliform; in *Lenzites* (Figs. 289 and 290) they are chiefly formed as definitely radiating lamellae (even though still tortuous), which from time to time anastomose leaving between them lengthwise slits where alone the hymenium develops. At the edge of the fructification, the partitions are often closer so that the hymenophore becomes more poroid. Occasionally the lamellae develop to serrate elevations and then appear quite similar to *Phlebia*. In the predominantly tropical *Favolus*, the lamellae are similar to those of *Lenzites* except that they anastomose regularly forming a faveolate network which is even more regular in *Hexagonia*. In *Cyclomyces*, the lamellae are arranged in concentric circles. *Favolus europaeus* is a parasite of nut trees, *Daedalea quercina* a parasite of oaks and chestnuts. *Lenzites saepiaria* cause a very serious decay of coniferous timbers in buildings, especially in America where it assumes the importance of *Merulius lacrymans* in Europe.

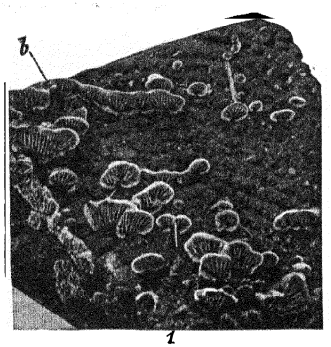


FIG. 290.—*Lenzites abietina*. Mussel shaped fructifications on fir beam. At *b*, several have coalesced to form a bracket. (Natural size; *after Falck*, 1909.)

As far as the representatives of this group have been investigated, *e.g.*, by Falck (1909), Zeller (1916), both in their natural habitats and in cultures (similar to the other Polyporaceae), they pass successively through

all stages of fructification formation occurring anywhere in the Polyporales. They first form arachnoid coverings, as those of *Hypochnus*, with the basidia on single hyphae; then the hyphae intertwine to single teeth, spines or plates, rising from the substrate; thereupon they join to form resupinate fructification similar to those of the Radulaceae; they then develop to bracket or centrally stipitate fructifications, sometimes to thelephoroid, or clavarioid, with poriform or elongate depressions, straight or daedaloid, finally ending in age as lamellate *Lenzites* fructifications. This example shows the impossibility of bringing these saprophytes or facultative parasites into a system, according to our present ideas of species.

Fistulinaceae.—This family is characterized especially by the structure of its hymenophore, which is covered in youth with independent

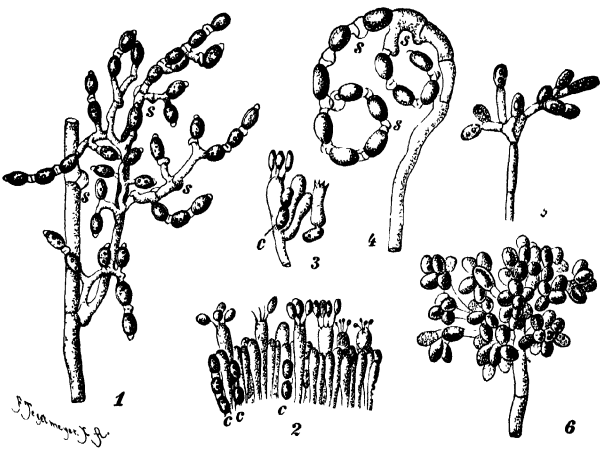


FIG. 291.—*Ceriomyces citrinus*. 1. Branched hypha, bearing gemmae. *s*, clamp connections. 2. Part of hymenium. Between the basidia lie hyphae with gemmae, *c*. 3. Basidia, bearing gemmae, *c*. *Fistulina hepatica*. 4. Gemmae-bearing hyphae. 5, 6. Gemmae-bearing hyphae of a fructification. (1 to 3, 5, 6 × 350; 4 × 400; *after Brefeld*, 1889.)

warty or granular elevations. These later elongate to peg-like tubes which are closed during growth and covered in the interior with hymenium; they open first at maturity. The phylogenetic connection of the family is obscure. The genus *Solenia* shows similar ontogeny. Maire (1902) connects it with the Polyporaceae and derives these from the Cyphellaceae.

The edible *Fistulina hepatica*, which forms brackets up to a half-meter on oaks, is best known. The hyphae in the interior are binucleate at first, becoming multinucleate by fragmentation. They are penetrated by latex vessels containing a dark red liquid. The upper surface of the fruc-

tification is covered by a gelatinous hyphal layer which swells much in damp weather. In the parts of the tissue lying beneath it, the hyphae of the context branch fruticosely during the young stage and at their ends cut off singly or in short chains, a large mass of thick-walled, ochraceous, binucleate gemmae (Fig. 291, 5 and 6). The flesh of the fungus is streaked dark and grayish by the large number of these gemmae. In the later stages of development, at the formation of the hymenium, formation of gemmae ceases (Seynes, 1874). The other species are confined to the southern United States.

CHAPTER XXVII

AGARICALES

The Agaricales include the gymnocarpous and hemiangiocarpous stage of the chiastobasidial Autobasidiomycetes. They are directly connected to the Polyporales especially to the Dictyolaceae (Cantharellaceae of most authors) and develop gradually in an angiocarpous direction where the hymenophore and hymenium develop successively in schizogenetically formed cavities within the fructification. The fructification is finally surrounded by a layer of tissue.

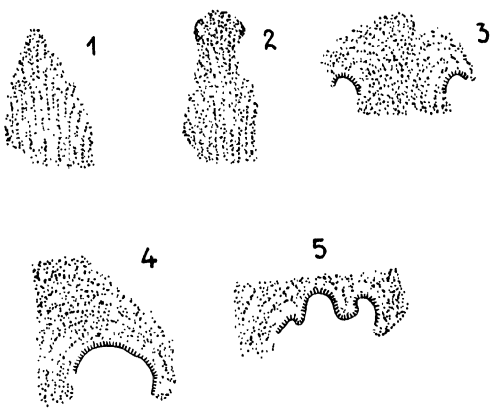


FIG. 292.—*Hygrophorous miniatus*. Diagrammatic sections of developing fructifications. 1. Young undifferentiated fructification. 2. Beginning differentiation into pileus and stipe. 3. Beginning formation of hymenium. 4, 5. Formation of lamellae. (× 20; *after Douglas*, 1918.)

The fructifications usually develop as centrally stipitate pilei. In contrast to those of the Polyporales, they are mostly transitory, perennation with annual addition of growth zones is unknown in them. They rise on mycelium or mycelial threads as knobs the size of a pin head, elongate subsequently in the direction of the main axis and differentiate into pileus and stipe.

In the lowest stage, the hymenophore, as in the Cantharellales and Polyporales, develops on the surface gymnocarpously (Fig. 292); the edge of the pileus, however, because of strongly epinastic growth, gradually arches toward the stipe so that its hyphae occasionally intertwine

with those at the edge of the stipe. Here belong some Hygrophoraceae and Clitocybeae.

In the middle stage the fundament of the pileus is always rolled up and its edge remains connected with the stipe primordium. Thus in the interior of the tissue an annular furrow, often with several chambers, encircles the fructification; in it the hymenophore is formed (endogenous, angiocarpous). The thin tissue, in the layer from the ground tissue connected to the stipe rind, which separates this cavity from the exterior and which, in a certain sense, is a continuation of the retroflexed margin of the pileus, is called the **partial veil** or **inner veil** (Fig. 293, *A*, *vp*). It is frequently evanescent. At maturity when the pileus expands by strongly hyponastic growth and general elongation of its hyphae, the partial veil is torn to shreds. Its remnants separate into threads and disappear, and only an ontogenetic investigation can show its original presence. Such an evanescent partial veil is found in many Lactariaceae, Marasmieae and Coprinaceae. In other cases, the partial veil acquires, from the edge of the pileus and from the stipe, new hyphal elements and consequently forms a stronger structure. Thus, in the expansion of the pileus, it is retained as such and is either loosened from the edge of the pileus (Fig. 293, *a*), or from the stipe. In the first case, it remains with the stipe in the form of a closely attached collar which is called the **inferior annulus** or ring. In the second case it remains hanging from the edge of the pileus; these remnants are usually called **cortina.** In some forms it is first loosened from the stipe, then from the margin and remains as a **movable ring** surrounding the stipe. The ring occurs in *Armillaria*, *Psalliota* and *Amanita*, a cortina in *Cortinarius* and *Hypholoma*, and a movable ring in a few species of *Coprinus* and *Lepiota*.

In the highest stage, finally, a cortical layer of mostly thick-walled hyphae, the membranous or blemmatogenous layer, is differentiated on the whole outer surface of young button. In most cases, as in the Tricholomeae and the Amaniteae, it remains connected with the tissue underneath (especially with the cortex of the pileus and the partial veil) and is only recognizable in cross-sections of young stages by its different appearence and staining capacity. At times it cannot follow the expansion of the pileus and remains on the pileus, as scales or as a powder or becomes a gel. In some genera, as *Amanita*, *Amanitopsis* and *Volvoboletus*, it is separated from the rest of the pileus by a swelling, sharply defined tissue and remains then in connection with the base of the often bulbous stipe only: this special peridial membrane surrounding the whole fructification like an egg shell, is called the **teleblem** (Fig. 293, *B*, *vu*). In individual cases it is covered by a loose flocculent layer which is called the **primary universal veil** or **protoblem.** The universal veil, not being able to follow the elongation of the stipe and the expansion of the pileus, is torn to pieces and then remains behind at the base of the

stipe, as sheath or **volva** (Fig. 293, *C*, *v*) and at the upper surface of the pileus, in the form of scales (*e.g.*, the white scales on the reddish pileus of *Amanita muscaria* (Fig. 293, *C*, *f*).

In this third type, the layer of the ground tissue corresponding to the partial veil undergoes a special development. Whereas generally the longitudinal axis of the lamellae forms an approximately right angle with the stipe axis, so that the partial veil is only contiguous to the stipe at its inner edge (somewhat as Fig. 293 *A*, *b*), occasionally in this third type, the two axes form a very sharp angle to each other. Consequently the lamellae run parallel to the stipe and the partial veil (the homologue) coalesces through almost its whole length with the rind of the stipe (Fig. 293, *B*, *ar*). It does not participate in the elongation of the inner stipe tissue, however, and at the expansion of the pileus, together with some

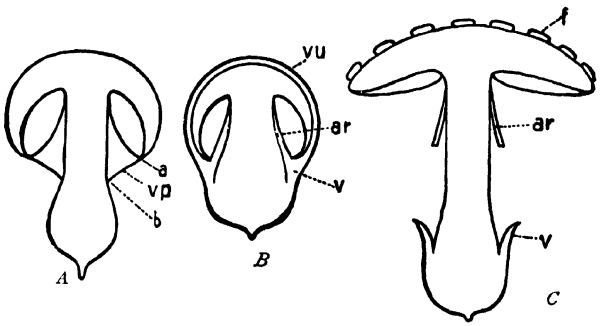


FIG. 293.—Diagram of two types of agaric fructifications. *A*. Immature fructification of second stage. *B*. Immature fructification of third stage. *C*. Unfolded fructification of third stage. (*After E. Fischer.*)

portions of the stipe rind, it is loosened from the stipe up to a narrow strip at the place of insertion of the pileus and spreads out with the pileus. Thereafter, it gradually becomes loosed from the edge of the pileus and the edges of the lamellae and hangs from the point of attachment in the form of a conical frill, broadening below (Fig. 293, *C*, *ar*). This ring, as its point of attachment lies higher than that of the earlier mentioned one, is called **superior annulus**, or **armilla.** Such an armilla is found in many species of *Amanita.*

The substance of the fructification is fleshy or fibrous in character, more seldom tough, horny or leathery. In the peripheral layers of tissues, it generally is firm and forms a highly differentiated pellicle. In many species, this pellicle (on the pileus) is separable from the ground tissue by a layer with gelatinized cell walls and is then easily separable or torn into scales. In others, it fuses directly with the substance of the pileus so that the increasing humidity in the fructification penetrates the underlying cells and often darkens them. These species are called hygrophan-

ous. Sometimes the pellicle is covered with cystidia-like cells, which at the edge of the pileus, gradually change to cystidia; possibly they function as hydathodes (Fayod, 1889; Istvaniffi, 1896; Knoll, 1912).

The elevation of the hymenophore is generally caused by the subhymenial hyphae, as those of the Polyporales, increasing their growth over the original surface of the fructification. In the lowest forms, *e.g.*, in the first gymnocarpous type, these elevations, as in the Dictyolaceae, spread out centrifugally from the annular furrow to the margin in the form of a few comparatively broad fleshy, or spongy folds. In the hemiangiocarpous (second and third) types, the development is more complicated and hence in part still controversial. In the (probably) simpler forms, the tramal hyphae grow from above into the annular furrow, and, under certain conditions, enter upon a temporary union with the opposite side of the furrow, the partial veil. In the higher forms, as *Amanita*, *Amanitopsis* and *Psalliota campestris*, the numerous cavities into which the tramal plates grow (horizontal in cross-section and running a distance around the fructification) are vertical and radiate regularly. The tramal plates are formed from the ground tissue. The lamellae in this highest type arise, not from renewed growth of the ground tissue which covers the cavity, but from the original ground tissue. Throughout the whole development they are connected with the peripheral ground tissue of the partial veil and become partially loosened from it only at maturity. Every individual cavity is laid down singly and schizogenetically.

In all these other angiocarpous forms, the lamellae are usually very numerous and very narrow; their characteristic structure has given to the order the name of gill fungi. The lamellae radiate and, in typical cases, are separate throughout their whole length. Only in a side line, which also differs in other respects (Paxillaceae, Boletaceae), are they connected by partitions into daedaloid structures. In contrast to the Polyporaceae, they proceed, in the higher forms at least, to form the hymenium when they have completed their growth and attained their final form. The hymenium forms over the whole fructification comparatively rapidly and simultaneously. Exceptionally, *e.g.*, in *Armillaria mellea*, basidia develop on the aerial mycelium, singly or in more compact layers which form a sort of hymenium.

The basidia correspond in form and development to the four-spored basidia of the Polyporales. Exceptionally in the lower forms *e.g.*, *Mycena* we find still a third step in the division of the basidial nucleus, without the spore number varying from four. Besides, in spite of the normal quadrinucleate condition of the basidia, in *Amanita bisporigera* two nuclei remain behind in the basidium (Lewis, 1906).

As imperfect forms, oidia have been observed in numerous genera, occasionally also conidia, gemmae or bulbils.

The Agaricales include approximately 100 genera with about 10,000 species. They are of fatiguing regularity and hence, despite the numerous unanswered questions, have been little studied from the point of view of comparative ontogeny. Actual systematic classification will be largely influenced by considerations of the herbarium systematist, and founded on the consideration of the color of the mature fructification and spores. The color of the spores in mass has offered assistance in the preparations of keys; the genera with white spores have been grouped as the Leucosporeae, those with violet brown spores as Amaurosporeae, those with brown (red or ochraceous brown) spores as Phaeosporeae, those with pinkish or flesh-colored spores as Rhodosporeae, and those with black spores, generally glistening violet, as Melanosporeae.

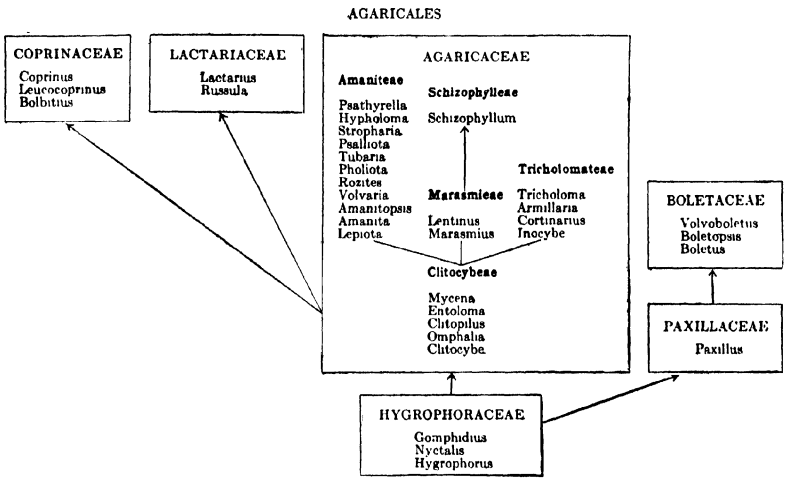


DIAGRAM XXIX.

A few representative genera of each of the seven families will be briefly discussed, but figures of the different species will be omitted because the necessary illustrative material, at least as far as it concerns edible or poisonous mushrooms, occurs freely in the numerous guides for mycophagists, as six of the families are more or less important as food: the Hygrophoraceae, mainly gymnocarpous forms with thick decurrent lamellae; the Lactariaceae, hemiangiocarpous forms without ring or cortina and with the peculiar rosette structure of the tissue of the fructification; the Coprinaceae, hemiangiocarpous forms with a characteristic structure of the hymenium; the Paxillaceae, mainly gymnocarpous forms with the tramal layer separable from the context; the Boletaceae (gymnocarpous or pseudohemiangiocarpous, whose tramal layer is separable from the pileus which, however, possesses tubes instead of lamellae;

and by way of an appendix, a still obscure family, the Hemigasteraceae, angiocarpous forms without lamellae. The seventh and largest family, that of the Agaricaceae, is entirely artificial and is mainly distinguished by a lack of marked characteristics. The especially striking morphological relationships between the families are shown on page 455.

Hygrophoraceae.—This family is connected with the Dictyolaceae both in structure and character of the fructifications; the elevations of the hymenophore are developed to true lamellae which rise freely, comparatively far apart, and have broad cross-sections (Battaille, 1910). They are alternately of different lengths; the longer ones are often decurrent; the surface of the pileus is slimy and the trama fleshy or waxy. As far as their ontogeny has been followed in detail, in *Hygrophorus* (*Hygrocybe*) *miniatus*, *H.* (*Hygrocybe*) *nitidus*, *H.* (*Camarophyllus*) *borealis* (Douglas, 1918), *H.* (*Limacium*) *Karsteni*, *H.* (*Limacium*) *agathosmus*, *H. Langei* (*H.* (*Hygrocybe*) *constans*) and *H.* (*Hygrocybe*) *nigrescens* (Kuehner, 1926), in the young fructification the lamellae develop exogenously in the annular furrow beneath the pileus fundament and centrifugally from the stipe. In the other species, *H.* (*Limacium*) *olivaceoalbus* (Kuehner, 1926) and *Gomphidius*, they appear to arise endogenously beneath an evanescent veil which extends from the edge of the pileus to the stipe.

The basidia show some primitive characters in their development. Thus in *Hygrophorus* (*Limacium*) *agathosmus* (as in *Neurophyllum clavatum*, p. 442), there are three divisions of the diploid nucleus although only four (occasionally only two) basidiospores are formed (Maire, 1902). The other nuclei remain in the basidium and perhaps are used in the formation of a second spore generation. A very peculiar cytological relationship was found in *H.* (*Hygrocybe*) *conicus* (*Godfrinia conica*) and *H.* (*Hygrocybe*) *Langei* in which the cells of the mycelium and fructification are bi- and multinucleate, while the cells of the hymenium and subhymenium only contain one nucleus each (Maire, 1902; Fries, 1911; Kuehner, 1926). The primary basidial nucleus divides only once (occasionally twice in *H. Langei*), both daughter nuclei lie directly under the top and gradually migrate into the middle of the basidium. Hereupon two sterigmata are formed, each of which cuts off a large reniform spore. Before or during the migration into the spores, both daughter nuclei again divide so that at separation, the spores are binucleate. While the two nuclei were seen lying close together in pairs in the trama, fusion was not observed, although the hymenial nuclei are much larger than those of the trama. The significance of this relationship may be more fully explained when the development of the primary basidial nucleus is better known. In *H.* (*Hygrocybe*) *nigrescens* (Kuehner, 1926), very closely related to *H.* (*Hygrocybe*) *conicus*, the young basidia are binucleate and the subsequent development is the usual one for this

genus. In *H.* (*Camarophyllus*) *virgineus* (Bauch, 1926) both four- and two-spored races are formed. The four-spored races develop normally with clamp connections and binucleate mycelia, while the two-spored race is always uninucleate and develops parthenogenetically. The haploid chromosome number is four in both races.

The basidiospores are smooth and hyaline except in *Gomphidius* where they are dark. Their germination was followed in *Nyctalis asterophora* (*N. lycoperdoides*) and *N. parasitica* parasitic on *Russula* and *Lactarius* (Brefeld, 1889). In these, they develop to mycelia which under certain nutritive conditions, produce oidia capable of immediate germination. In time, oidial formation disappears and is gradually replaced by thick-walled, brown or ochraceous gemmae which are rich in reserve materials. In *N. parasitica* the gemmae are mostly intercalary and smooth, and in *N. asterophora* they are terminal and echinulate or verrucose. They are liberated by swelling of the intermediate cells. In natute, they are formed in the lamellae in *N. parasitica* and in the peripheral layers of the pileus in *N. asterophora*. They are produced in such numbers that the lamellae below the pileus are stunted or only suggested, and never mature. In small individuals, the fundament of the fructification does not extend much above the thick mass of gemmae which have an odor like that of rancid meal. Under suitable cultural conditions, the gemmae may germinate to mycelia.

Agaricaceae.—This family differs from the Hygrophoraceae by the higher development of its thin lamellae; the trama becomes very thin so the lamellae consists mostly of the two hymenia. Otherwise, the characters are mostly negative. To this family are assigned all those forms which for lack of special characters cannot be placed in the other families. In this sense, they include at least eight thousand species which one, according to his taste, may divide into a varying number of tribes and genera. Five of these tribes with about two dozen genera are briefly discussed.

The Clitocybeae or Collybieae form a direct continuation of the Hygrophoraceae. They are also strongly reminiscent of the Cantharellaceae and Dictyolaceae and pass over so gradually that *Clitocybe auranti-aca* is often considered a species of *Cantharellus*. Their fructifications are fibrous or fleshy, their lamellae are membranous; in part these are still decurrent and in the majority of species are exogenous, as in *Hygrophorus*. In others, however, as in *Gomphidius*, they are formed endogenously within a partial veil. The first-named type was shown for *Mycena subalcalina*, *Entoloma flavifolium* (Douglas, 1918), *Omphalia chrysophylla*, *Clitocybe cerussata*, *Clitopilus noveboracensis* (Blizzard, 1917) and *Pluteus admirabilis* (Walker, 1919), *Collybia tuberosa* and *C. velutipes* (Moss, 1923), *Mycena pterigena*, *M. sanguinolenta*, *M. codoniceps* (Kuehner, 1926), and the latter type for *Clitocybe laccatus* (*Laccaria laccata*) (Beer,

1911), *Omphalia integrella* (*Delicatula integrella*) and *Leucopaxillus paradoxus* (*Clitocybe paradoxa*) (Kuehner, 1926).

The basidia belong mostly to the four-spored type; the diploid nucleus, *e.g.*, in *Mycena galericulata*, shows the primitive position of this tribe by three divisions, as in *Hygrophorus agathosmus* (Maire, 1902). The two-spored forms resemble *Hygrophorus conicus* and *H. virgineus* in that the spores develop parthenogenetically from uninucleate basidia and subhymenial cells (Kuehner, 1927). The basidiospores are smooth or echinulate. Oidia have been demonstrated for *Collybia velutipes* (Biffen, 1899); sclerotia have been found in *Collybia*. In biological relations, *Collybia eurhiza* is of special interest as it is cultivated by termites in their nests in Ceylon and Java, like the South American *Rozites gongylophora*.

Many of the species are edible.

The *Marasmieae* are an artificial group in which forms similar to those of the Clitocybeae are grouped. They are tough, persistent, collapsing in dry weather and reviving on return of humid conditions, membranous, horny or even woody. The basidiospores are hyaline and smooth.

The two best-known genera are *Lentinus* and *Marasmius*. In *Lentinus*, the lamellae are adnate, in *Marasmius* they are free. Further, in *Lentinus* the tramal hyphae project in the form of fringe or teeth. The edge of the lamella resembles a saw. This group is largely tropical. In Europe *Marasmius oreades*, which resembles a *Collybia*, is used for food. *Marasmius perniciosus* attacks *Theobroma Cacao* in Surinam, *M. plicatus* and *M. Sacchari* causes the root disease of sugar cane in Java.

Schizophylleae.—The only well-known species of this tribe, *Schizophyllum commune* has long held an anomalous position in the Agaricaceae, and it seems probable from the studies of Essig (1922) that it should be transferred to the Cyphellaceae, or to the vicinity of *Cladoderris* in the Corticiaceae or Radulaceae. Adams (1918) reported that the hymenium was formed as a lining of radiating cavities, which finally split open. Essig was unable to confirm these observations. The stipe may be either central or lateral, but is always on the side of the pileus opposite the hymenium, as in the Cyphellaceae. The mycelium is provided with clamp connections and is binucleate throughout its development, since the spore is binucleate. The fructification develops as small clavarioid tuft with an apical pore. The hyphae just behind the apex differentiate into the hymenial palisade, which expands and pulls apart the hyphae of the tip. In this stage it resembles a large *Cyphella* or a *Peziza*. The "lamellae" arise as short isolated ridges upon the surface of the hymenial primordium. The primary ridges arise successively from a point beneath the attachment of the stipe and radiate outward until they fuse with the margin of the pileus. The secondary "lamellae" arise between them and are not attached to the primary ones as sometimes reported. The

palisade layer splits over these ridges as it often does in *Cladoderris*, and the edges grow downward, followed by a growth of the hymenial plates. This growth continues throughout the life of the fructification. Earlier authors, as Fries, Fayod (1889) and Buller (1909), had supposed that the lamellae were first formed and later split due to hygroscopic tension. While *Schizophyllum commune* is a weak wound parasite, it is probable that most of the damage attributed to it is caused by other Basidiomycetes which grow more slowly and hence do not reveal their presence by production of fructifications as soon as this species.

Tricholomateae.—This tribe is connected to the higher Clitocybeae from which it is often difficult to separate. Some species whose lamellae are separable from the pileus (*e.g.*, *Cortinarius largus*) remind one of the Paxilleae. *Tricholoma nudum* (*Rhodopaxillus nudus*) and *T. Georgii* are gymnocarpous (Kuehner, 1926). The partial veil is retained in some genera, in *Armillaria* as a ring and in *Cortinarius* as a cortina. As far as the ontogeny of the fructifications has been investigated, as in *Inocybe* (Douglas, 1920), *Cortinarius* (Douglas, 1916; Sawyer, 1917; Kuehner, 1926) and *Armillaria* (Fischer, 1909; Beer, 1911; Atkinson, 1914, 1915), a blemmatogenous layer is differentiated at the periphery of the fundament of the fructification. This layer generally remains connected with the underlying layer of tissue, particularly in the pileus and partial veil; the remnants may be observed as scales on the upper surface of the pileus after the expansion of the fructification.

Armillaria mellea (*Clitocybe monadelpha*, *Armillariella mellea*) has an enormous economic significance as a destroyer of forests. Its brown to black rhizomorphs, often anastomosing to layers of tissue in tree trunks, at times phosphorescent, spread through the ground for considerable distances. They send slender hyphae which penetrate the collar and the roots of frondose species, destroy the cell walls at the butt and cause a white rot of the wood and the death of the tree.

Amaniteae.—In this tribe, the Agaricaceae reach their highest point. Differentiation has proceeded further than in the previous subfamilies: pileus and stipe differ from each other in structure and usually may be easily separated from each other. In all genera recently investigated, as in *Hypholoma* (Allen, 1906; Beer, 1911), *Tubaria* (Walker, 1919; Kuehner, 1926, *Lepiota* (Atkinson, 1914), *Myxoderma* (*Limacella*, *Lepiota*) (Kuehner, 1926), *Pholiota* (Sawyer, 1917) *Rozites* (Kuehner, 1926), *Psalliota* (Atkinson, 1906, 1914, 1915; Levine, 1922), *Stropharia* (Zeller, 1914; McDougall, 1919), *Amanitopsis* (Atkinson, 1914, 1915) and *Panaeolus* (Kuehner, 1926), the development of the fructification takes place, as in the Tricholomateae, hemiangiocarpously. In *Amanitopsis*, the blemmatogenous layer is differentiated into a true universal veil.

The subfamily is divided into several parallel series, first recognized by Patouillard (1900), which, however, in many respects are in need of

consistent working out. The series of Amanitinae includes fleshy forms whose spores possess no germ pore, as *Lepiota* (white spored, with ring, without volva), *Amanita* (white spored, with ring and volva), *Amanitopsis* (like *Amanita* without ring) and *Volvaria* (pink spored without ring with volva); the Pholiotinae includes similar types with ochraceaous spores, with or without germ pore, among the fleshy forms *Rozites* (spores warty), *Pholiota* (spores smooth), among the cartilaginous forms *Tubaria* (lamellae decurrent); the Agaricinae with spores of various colors (not ochraceous) with a germ pore, *Psalliota* (with ring, cap separable, spores brown) *Stropharia,* (like *Psalliota,* pileus and stipe not separable), *Hypholoma* (with cortina, spores as *Psalliota*), *Psathyrella,* spores black, etc.

Biologically, one species of *Rozites* is especially interesting. *R. gongylophora* (Möller, 1893) in Brazil is cultivated by several genera of ants, especially the leaf-cutting species (*Atta* sp.), in subterranean labyrinthine fungus gardens. The substance of these spongy masses consists of an enormous number of little globules of up to ½ mm. in diameter which are formed from the kneaded-together remains of leaves which the ants have carried into their nests as substrate for their fungi. In freshly made spots they are dark green, in older almost black, and in still older yellowish brown; they are permeated and loosely held together by white hyphae. In the upper surfaces of the gardens, the hyphae join into small fascicles measuring about 1 mm.; their ends become clavate and filled with highly refractive protoplasm; these groups form the chief, if not the only food for these ants. If the ants are removed and the gardens abandoned (as also in artificial cultures) aspergilloid conidial chains are cut off from the slightly clavate branches of the thick aerial mycelium. In poor nourishment, peculiar pockets appear on the hyphae, and the conidial fructification passes into a second stage with more oval conidia which are cut off in long chains directly from the hyphae.

It is noteworthy that in the cultivated strains of *Psalliota campestris,* the basidia are mostly two-spored, in the wild strains usually four-spored. Perhaps the two-spored condition is a sign of degeneration in the cultivated strains.

Lactariaceae.—This natural family is characterized by decurrent, comparatively thick, fragile lamellae and rough, echinulate, mostly colorless spores. The tissue of the fructification, above all of the trama, consists of a mixture of ordinary hyphae and of sphaerocysts generally arranged in rosettes, thus appearing vesiculose to the naked eye. The sphaerocysts are swollen, originally binucleate, hyphal cells, filled with clear liquid, whose nuclei fragment. Their ontogeny and function is still unknown.

In *Lactarius rufus* (Kuehner, 1926), the young primordium is differentiated into an outer layer of vacuolate hyphae and an axis of slender hyphae with prominent nuclei and reserves at the base of the fructification.

Gradually there is formed near the top an annular furrow and the rosettes of sphaerocysts begin to appear in the interior of the stipe portion. The lactiferous ducts develop in the surface of the stipe and in the context of the pileus, perhaps derived from the auxiliary hyphae. At the upper end of the stipe the palisade, intermingled with sharp binucleate cystidia, gradually grows out over the lower side of the pileus as it expands. Sphaerocysts then appear in the pileus and the lamellae begin to form. Thus, in this species at least, development is strictly gymnocarpous and quite comparable to that of the Polyporales.

In *Lactarius deliciosus* (Maire, 1902), the diploid nucleus divides twice, and immediately after migration into the spores, the daughter nuclei divide a third time. Imperfect forms have not yet been observed. Only in *L. sanguifluus* do the hyphae appear to form gemmae on short branches (Rouge, 1907).

The family includes only two genera, *Lactarius*, whose fructifications are permeated by latex vessels and hence on wounding exude a turbid, often colored liquid, and *Russula*, whose fructifications lack these vessels. Numerous species belonging here are palatable and prized as food.

Coprinaceae.—This family is reminiscent of the simpler Agaricaeae in the structure of its fructification (Levine, 1914; Atkinson, 1916; Kuehner, 1926). In the lower forms, the partial veil is evanescent, in higher forms it is retained as a ring, and in the highest it is covered by a blemmatogenous layer, occasionally by a universal veil. In contrast to the Agaricaceae the pileus does not expand at maturity like an umbrella but because of lack of geotropic stimulation, hangs campanulately from the place of attachment at the stipe. The lamellae are thin and weak, at times not over 200μ thick, often hygrophanous and subject to rapid deliquescence, as is the whole fructification. In a few species, as in *Coprinus comatus* and *C. sterquilinus*, they are held apart by a thickening of the rim and prevented from sticking together: in others, as *C. atramentarius*, they are separated by large, projecting cystidia (75 to 100 per square millimeter) which reach the opposite side of the interlamellar space and bore firmly into the trama (Fig. 294, 1) (Buller 1910).

The basidia do not stand, as in most other Agaricales, uninterruptedly beside each other, but they are separated by numerous, regularly arranged "paraphyses." They belong to the usual four-spored type; in many species, as *C. comatus*, *C. atramentarius*, *C. stercorarius* and *C. ephemerus*, they are constructed in two forms, one long, one short (Fig. 294, 2). The significance of this dimorphism is still obscure; it is noteworthy that the long basidia shed their pores earlier than the short (Buller, 1915).

In contrast to the other Agaricales, maturation of the basidium does not take place simultaneously over the whole fructification, but gradually inwards from a small zone at the margin of the pileus. One can, as Buller (1909), designate the general Agaricales type as the Equihymenial

type or, according to the best-known example, as the *Psalliota* type, and distinguish this as the Inequihymenial or *Coprinus* type, which should not be confused with the earlier described ontogeny of the Polyporales. In the latter, the hymenophore begins the formation of the basidia before the fructification has attained its final form and before the folds and elevations of the hymenophore are laid down. The trama occasionally continues its growth for months and thus adds new and younger lateral elements to the hymenophore and hymenium. In the *Coprinus* type, as in the other Agaricales except the Lactariaceae, the hymenium is formed

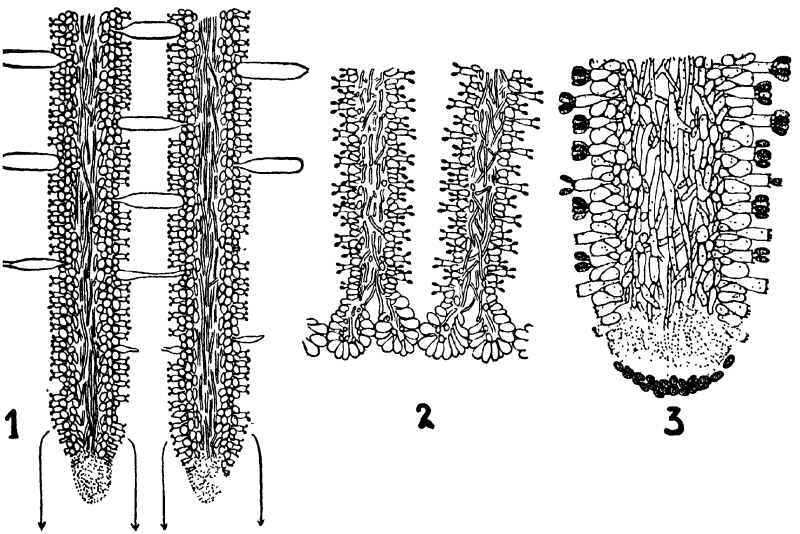


FIG. 294.—*Coprinus atramentarius*. 1. Section of two lamellae with supporting cystidia. Autolysis beginning (× 75). *Coprinus sterquilinus*. 2. Section of two immature lamellae with thickened ends and dimorphous basidia. Cystidia absent (× 43). 3. Section of a lamella of mature fructification. Spore liberation and autolysis have begun (× 120). (*After Buller*, 1910 and 1915.)

over the whole hymenophore after the tramal plates have completed their growth. The difference between the *Coprinus* and *Psalliota* type, therefore appears only at maturity of the individual basidia in the spore discharge, which in the former takes place in steps from the periphery (Fig. 294, 1 and 3), in the latter evenly over the whole hymenial surface.

Along this zone of mature basidia in *Coprinus*, an enzymatic autolysis of the exhausted lamellae proceeds from the edge of the pileus to the stipe. The margin bends outward and upward and the tissue dissolves to an inky liquid which gradually drops from the fructification (Weir, 1911). Probably this peculiar condition is connected with the structure and orientation of the lamellae. While the lamellae in many agarics have a

triangular cross section below, *e.g.*, grow narrow toward the edge and leave open a widening space for the spores to fall through, in the Coprinaceae the walls are parallel and the space for discharge and fall is just as narrow at the distal end as at the proximal. Further, the lengthwise axis of the lamellae in mature fructifications does not lie parallel to the ground, as in many other Agaricales, but is more or less perpendicular to it. Since this axis runs in the direction of fall, a spore under some conditions would fall several centimeters along its surfaces. There is danger that the spores in question may hit the cystidia or the lamellae and thus fail to reach their destination to allow dispersal by wind. By this differential maturing of the spores and the immediate subsequent autolysis of the exhausted tissue, there is an elimination of those parts of the lamellae which have already fulfilled their function and whose longer presence would hinder the fall of the remaining spores. The cystidia are autolysed somewhat earlier (often less than a half hour) than the remaining tissue. The fact that in those species in which the lamellae spread at the expansion of the pileus, *e.g.*, in *C. niveus*, autolysis is weak and limited to the edge of the pileus, also points to the correctness of this interpretation of autolysis.

The basidiospores are thick walled and provided with a terminal germ pore. Their germination was discussed in detail on page 397. In some species, as *C. ephemerus* and *C. lagopus*, there occasionally arise on the primary mycelia small fascicles of short side branches which, as in numerous other Basidiomycetes, break up into bacilliform oidia. Generally these oidia are formed in such large masses that they obscure the cultural characters (Brefeld, 1877). In some species, as *C. stercorarius*, the hyphae later intertwine to dark-coated sclerotia up to the size of hazel nuts which, under certain conditions, develop to fructifications.

The Coprinaceae may be divided into two genera, *Coprinus* (spores black or brownish black) and *Bolbitius* (spore ochraceous, yellow under the microscope). The majority of these two genera are found on dung. Many are palatable when young, as *Coprinus comatus*, the shaggy mane.

Paxillaceae.—In this family the lamellae are easily separable from the pileus; as, however, this character appears occasionally in other families, especially the Clitocybeae, its consideration as a separate family is open to question. Its significance lies in the fact that in many species the lamellae, particularly at the fundament of the stipe, anastomose like veins and finally fuse to Polyporaceous tubiform networks (*e.g.*, *Paxillus rhodoxanthus*). This peculiarity forms the point for the connection of the Boletaceae which are always tubiform and hence generally placed beside or in the Polyporaceae, although their ontogenetic characters suggest the Agaricales.

In their present provisional limits the Paxillaceae ascend from resupinate to infundibuliform and finally Agaricaceous, apparently gymnocarpous fructifications. Their flesh is firm; the lamellae are decurrent and membranous. Some species are used for food.

Boletaceae.—The fructifications are always pileate, and centrally stipitate. The tube layer is easily separable from the flesh of the pileus. Many species contain fat reservoirs in special hyphae from which on injury flows a colorless fluid which colors intensely in air. The basidia correspond to the usual four-spored type. The young nucleus in all species so far studied passes through its usual division shortly after its entrance (Levine, 1913).

In *Boletus Zelleri* (*Ceriomyces Zelleri*) (Zeller, 1914) and *Boletus parasiticus* (Kuehner, 1926) development is gymnocarpous. In *Boletus flavus* (*Ixocomus flavus*) and *Boletinus cavipes* the annular furrow is at first on the surface then in the young stage, the hyphal tissue of the margin of the pileus is continued in a more or less definite partial veil to the rind of the stipe and the tubes and the hymenium arise with an arched annular cavity. Basidia and spores are produced in a hymenium which covers the top of the annular furrow before the tubes are formed, as in the Polyporales (Kuehner, 1926, 1927*a*). In most species the remains of the veil disappear in the course of development so that the mature condition is no longer reminiscent of the pseudohemiangiocarpous young stage. In others in which it is strongly formed, as in *Boletinus cavipes* and *Strobilomyces*, remnants remain on the stipe as a ring, or on the margin of the pileus as a cortina. In still others, unfortunately imperfectly known genera, *e.g.*, in *Volvoboletus*, a universal veil is differentiated as in the Amaniteae in the formation of the fructification.

All these characters raise the Boletaceae above the Polyporales in which they were usually placed and place them among the Agaricales. These relationships are reinforced in that the Boletaceae also histologically stand considerably higher than the Polyporales and here again have attained the stage of the Agaricales (Yates, 1916).

Patouillard (1900) and Maire (1902)—who have been followed in this book—advocated that the Boletaceae should be connected to the Paxillaceae, in the Agaricales, where the tramal layer also is easily loosened from the flesh of the pileus. This removal indicates a further step in the recognition that the lamellae and tubiform tramal plates are of secondary importance in a systematic treatment of the Basidiomycetes, and that a natural classification of this order can be completed only with histological and cytological characters.

Many species are edible.

As an appendix to the Agaricales, *Rhacophyllus lilacinus* on dead wood in the tropics should be considered, since it undoubtedly has affinities with this family, although its ontogeny and cytology are only partially

known. Superficially the fungus resembles an agaric but produces sheets of biconvex bulbils in the place of lamellae. The mycelium develops readily from bulbils on blocks of porous wood which are not too wet. The stipe primordium of large and longitudinal hyphae is early developed. The pileus is covered by a universal veil. Trabeculae, the primordia of the lamellae, extend from the pileus to the ground tissue, but no annular gill cavity is formed. The pileus becomes broadly conical, the tissue between the pileus and the stipe begins to produce bulbils, which arise singly, not in continuous sheets. They are of loose texture at first, often hollow and lined with a palisade layer or, if solid, with two opposed palisade layers in the center. The cells of the palisade layers produce cylindrical or oval spore-like cells at their apices within the

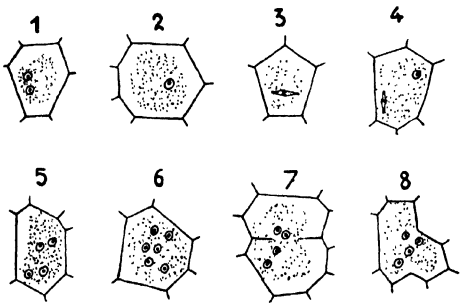


FIG. 295.—*Rhacophyllus lilacinus*. Caryogamy and plasmogamy in the bulbils. (*After Moreau*, 1913.)

developing bulbil. These cells do not become free but remain united in short chains. The bulbils never include hyphae of the ground tissue and at maturity are shed instead of spores (Petch, 1926).

While in the normal agaric the gill primordia develop into plates of tissue which produce palisade layers of basidia externally relative to the primordial tissue; in *Rhacophyllus* the "gill primordium" or trabecula develops a palisade tissue internally from either side, like the hymenium of the Gasteromycetes.

The bulbils contain mostly binucleate cells. The nuclei approach and fuse (Fig. 295, 1 and 2), the resulting nucleus divides twice so that there are four nuclei. Two of the four nuclei degenerate and the primitive nuclear number is restored. Thus the nuclear behavior is similar to that of a basidium (Moreau, 1913).

Often the septa dissolve and the protoplasts fuse (Fig. 295, 7 and 8). The material on which these studies were based was such that further details were not obtainable. Here apparently we have groups of basidia (or perhaps spores) taking the place of normal basidiospores in reproducing the organism. The relationships of this genus are very obscure. A

single collection by Duss from Guadaloupe contained a specimen of *Psathyra* near *P. gyroflexa*, but with no indication that it came from the same mycelium. Subsequent field studies over a long period by Petch have failed to find a normal agaric growing with this genus. While superficially *Rhacophyllus* resembles the agarics, its ontogeny suggests rather Gasteromycetous affinities, such as *Podaxon*, *Gyrophragmium*, etc., but none of these genera have been sufficiently studied to determine relationships.

Hemigasteraceae.—As an appendix, we have retained this interesting form in the position suggested by Juel (1895) although it might be interpolated in the developmental series leading to *Secotium* in the Hysterangiaceae as suggested by Gäumann (1926). Its development suggests that of *Boletus flavus* on a smaller scale. In *Hemigaster candidus*



FIG. 296.—*Hemigaster candidus*. 1. Coremium of diverging hyphae which form the fundament of the pileus. 2. Older stage. Pileus more distinct, with the young hymenium below. 3. Immature fructification. On the sides of the middle column grow the gemmae-forming hyphae. (1, 2 × 50; 3 × 27; *after Juel*, 1895.)

on rabbit dung in Sweden, the fundament of the fructification consists of a spherical knob of closely intertwined hyphae (Fig. 296, 1) which extend to the top of the head, almost parallel, then outward and downward. The tips bend downward at a right angle on the lower side, forming the fundament of the hymenium (Fig. 296, 2). Eventually the hyphae on the margin of the pileus grow to and fuse with those of the stipe, forming a closed annular chamber (Fig. 296, 3). The outer layer of the pileus differentiates into a loose outer and a firm inner layer surrounding the pileus. The outer two thirds is occupied by hymenium consisting exclusively of four-spored basidia with small, smooth, ellipsoidal spores. The inner third is filled by a hyphal tissue which grows from the stipe within the annular furrow and develops on lateral branches, numerous, sub-sessile, occasionally catenulate gemmae. In the following period, the head containing the chamber expands horizontally and is almost filled by increasing masses of gemmae. At maturity, the gemmophores disintegrate and the chamber contains a powder of free basidiospores and gemmae.

CHAPTER XXVIII

GASTEROMYCETES

This traditional group of fungi, originally contrasted with the Hymenomycetes, includes an assemblage of families of angiocarpous Autobasidiomycetes which undoubtedly belong to several developmental series. Lack of ontogenetic investigation prevents a satisfactory regrouping up to the present although numerous attempts have been made. These attempts have been based upon too few data to justify themselves. The segregation which has survived the longest was based upon the arrangement of basidia, but, like similar segregation of the Hypochnaceae for a few species of *Hypochnus* and *Corticium*, this segregation of the Plectobasidiales (Fischer, 1900) is untenable. It consisted in removing the Podaxaceae, the Sclerodermataceae, the Calostomataceae, Tulostomataceae and the Sphaerobolaceae from the Lycoperdaceae and Nidulariaceae in their broader limits and erecting them into a single polyphyletic order, on the basis of single character.

In the Gasteromycetes, the hymenia arise on irregular plates of tissue anastomosing to form a chambered, fertile tissue called the **gleba,** which is usually surrounded by a cover of sterile tissue called the **peridium.** The basidia are mostly four, occasionally two to three or six to eight spored and, except in *Tulostoma*, develop chiastobasidially as far as known. In all forms previously studied, as *Lycoperdon excipuliforme*, *Geaster fimbriatus*, *Nidularia farcta* (*N. globosa*) (Maire, 1902), *N. pisiformis* (Fries, 1911), *Cyathus striatus* (*C. hirsutus*) (Maire, 1902), *Secotium novae-zealandiae* (Cunningham, 1925) and *Lycoperdon depressum* (Cunningham, 1927) the nucleus divides soon after it enters the spores, so that the mature spores and all the resulting mycelium is binucleate. In *Nidularia*, especially in impure or poorly nourished cultures, the hyphae tend to break up into oidia. Apparently oidia are produced in the outer layer of the peridium of *Arcangeliella caudata* (Zeller and C. W. Dodge, 1919), although no attempt was made to germinate them. In *Leucophlebs*, which probably represents the conidial stage of *Leucogaster*, clusters of conidia on rather elaborate conidiophores fill the cavities of the fructification before the formation of the basidia.

The primitive members of the group are mostly hypogaeous, although there is a strong tendency to elevate the gleba above the earth to secure the dissemination of their spores by wind or insects. With the complete angiocarpous development of the hymenium, the original mechanism of

the basidium to secure spore dispersal has been lost and its function assumed by the fructification as a whole, *e.g.*, by the odor attracting rodents which eat the fructifications and disperse the spores in their feces, by the dustiness and capillitium of the gleba which enables pressure by wind or animals upon the sides of the fructification to puff out a cloud of spores, whence the name puff-balls, or by the elevation of the gleba upon a stipe, attracting insects which carry away the spores from the autolyzing gleba.

The peridium in the lower forms is a simple layer of plectenchyma undifferentiated from the ground tissue of the developing fructification. From these we may get a gradual disappearance of the peridium or its differentiation into several layers with varied and important ecological functions.

The Gasteromycetes are a mixture of various genera which possibly belong to entirely different development series. The following classification rests upon the differences in the place of the hymenial fundament and the direction of growth of the tramal plates. The first group in which the hymenium is formed in thick, more or less isodiametric knots of tissue (which have arisen by the pulling apart of the ground tissue) almost simultaneously from the center outward, throughout the whole fructification, includes the Rhizopogonaceae, Sclerodermataceae and Lycoperdaceae. A second group, in which the hymenium arises within a few closed chambers isolated at maturity, includes the Sphaerobolaceae and Nidulariaceae. In the third group the tramal plates are regularly arranged, start at definite points and grow in a definite direction. In the Hymenogasteraceae they grow basipetally, in the Hysterangiaceae and Clathraceae they grow centrifugally from a central part and in the Phallaceae, centripetally from the periphery.

Rhizopogonaceae.—This family includes hypogaeous or epigaeous genera with a gelatinous gleba of schizogenetic cavities. The fructification is surrounded by a surface layer of ground tissue (simplex peridium of Zeller and C. W. Dodge, 1918), or by a more or less differentiated peridium outside the ground tissue (duplex peridium of Zeller and C. W. Dodge).

One of the more primitive forms is the cosmopolitan *Rhizopogon rubescens*. Its fructification arises as a small knob, on a slender mycelial thread, whose rind becomes the peridium and whose core, which consists of hyphae of variable thickness, continues in the ground tissue of the fundament (Rehsteiner, 1892). The ground tissue is differentiated by a separation of the hyphae into compacter and looser tissues. The looser parts which run between the thicker knots, become still looser and finally form irregular cavities which are penetrated by single, thick, septate hyphae. From the periphery (Fig. 297, *C*), new hyphal knots are continually differentiated along with the increasing growth of the fructifi-

cation. Subsequently, the hyphae of the surface of the cavities come together into a hymenial palisade. By growth of the palisade, the tramal plates become increasingly irregular and finally occupy most of the gleba (Fig. 297, *B*).

In some species, as *R. luteolus*, the trama tend to split, suggesting conditions in *Pisolithus* in the Sclerodermataceae. In other species there is differentiated, outside the ground tissue, a peridium which may be

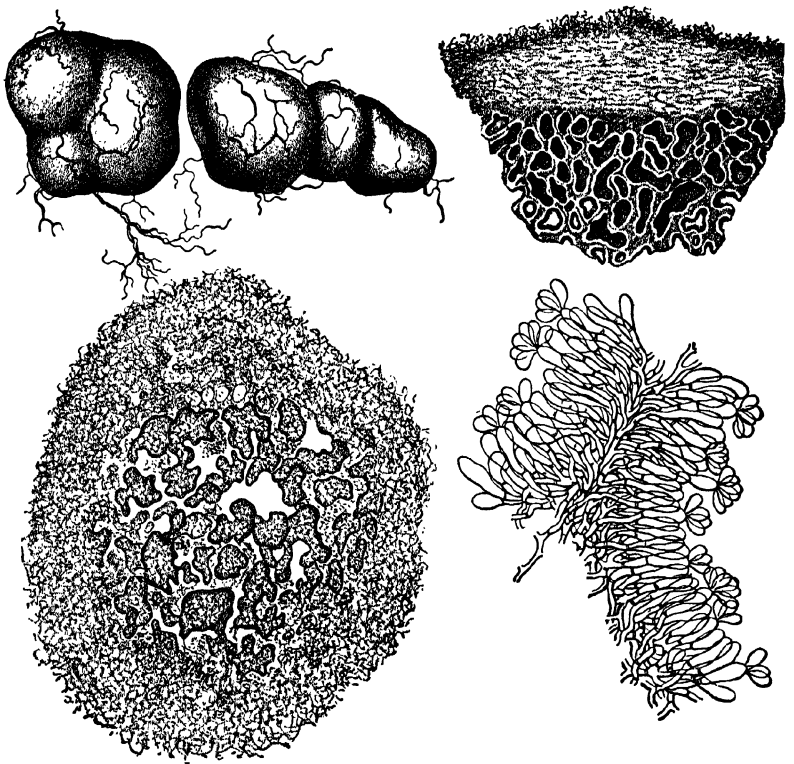


FIG. 297.—*Rhizopogon luteolus*. *A*. Habit (natural size). *B*. Portion of periphery of fructification (× 14). *C*. Part of gleba (× 450). *Rhizopogon rubescens*. *D*. Median section of young fructification (× 28). (*After Tulasne and Rehsteiner.*)

evident only by the different character of the cells (swollen and irregular in *R. diplophloeus*) or by different color and its sloughing off in spots, giving a characteristic ragged appearance to the fructification, as in *R. pannosus* and *R. Briardi*.

Melanogaster variegatus is similar to *R. rubescens* in appearance, but its spores are black instead of light yellow and its basidia are short, pyriform and not arranged in compact hymenia. The latter character led some

authors to place this genus in the Sclerodermataceae. It seems to be a transition form in many of its characters but it has not been investigated ontogenetically nor cytologically.

In *Leucogaster* we have another interesting genus, perhaps even more primitive than *Rhizopogon*. As in *R. rubescens*, the cavities develop centrifugally from the ground tissue. In *L. floccosus* the cavities are first filled by spores borne acrogenously on short branches of zigzag hyphae, or sometimes terminally on large hyphae springing from the trama. These consititute the *Leucophlebs* stage which is also known in *L. odoratus*, *L. foveolatus* and *L. citrinus*. If these are not disseminated they disintegrate *in situ*, filling the cavity with a dilute gel into which the basidia penetrate. The basidia are sometimes long pedicellate, pyriform, often with pedicels 200 to 300μ long, and solitary in *L. araneosus* and *L. rubescens*. In other species, as those of Europe and *L. citrinus* of California and Australia, the basidia are short and united into compact hymenia. The

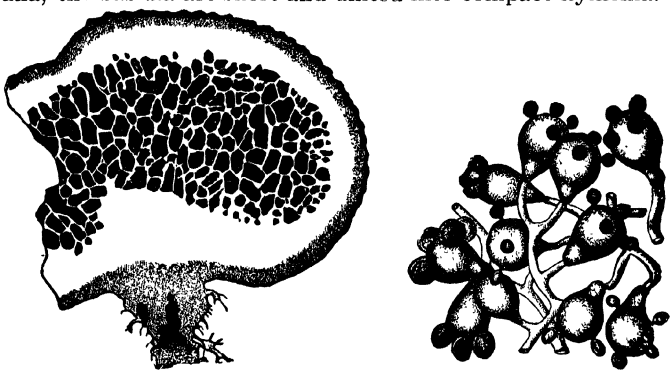


FIG. 298.—*Scleroderma vulgare*. A section of young fructification. *B*. Portion of gleba. (*After Tulasne.*)

spores are very highly sculptured and enclosed in a gelatinous sheath. A true peridium is only developed in *L. luteomaculatus* and even here it is not so highly differentiated as in some species of *Rhizopogon*. Many features of this genus are suggestive of the Sclerodermataceae, but unfortunately it has been little studied.

It is possible that other genera which have not yet been studied ontogenetically may belong here, but such fragmentary statements as have been made lead one to classify them elsewhere for the present.

Sclerodermataceae.—This family includes a group of simple forms with a simple peridium which splits irregularly at maturity (except in *Scleroderma Geaster*) and a chambered gleba, penetrated by a slightly developed capillitium, and becoming dusty at maturity. The fructifications of *S. Bovista* and *S. vulgare* are usually epigaeous, arising laterally or terminally on mycelial threads, from a homogeneous tissue of thin-walled, tangled hyphae which radiate toward the periphery. These

hyphae form the fundament of the coarse fragile peridium, usually scaly on the outside, and quite distinct from the gleba. At numerous points on the ground tissue, the hyphae branch more strongly, intertwine within (Fig. 299, 1, *Kn*) and rise as dark, deeply staining knots from the surrounding undifferentiated ground tissue (Rabinowitsch, 1894). The knots are loosened later with the swelling of the hyphae whose branches are directed toward the middle of the knot. These terminal cells become

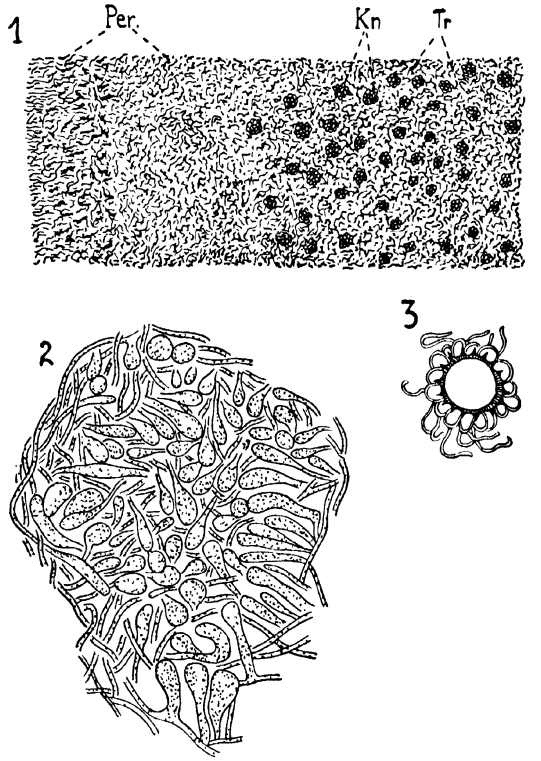


FIG. 299.—*Scleroderma Bovista*. 1. Median section of periphery of young fructification. *Per*, peridium; *Kn*, knots of hyphae; *Tr*, tramal hyphae between the knots. 2. Knot at the beginning of basidial formation. 3. Basidiospore with nurse hyphae. (1 × 65; 2 × 375; 3 × 570; *after Rabinowitsch*, 1894.)

basidia (Fig. 299, 2) which absorb the content of the knot hyphae, so that during the later development of the basidia there are no traces of the knot fundaments. The vacuolate, collapsed hyphae of the ground tissue surround the spores and cling to them so that these are more or less covered with a thick sheath of intertwined hyphal cells (Fig. 299, 3). At maturity the gleba disintegrates into a powdery mass with a few hyphae remaining behind as a simple capillitium; finally, the peridium

ruptures irregularly and the spores are blown away by wind or washed away by rain.

In the cosmopolitan *Pisolithus* (*Polysaccum*), the fructifications are similarly formed but the maturing process takes place basipetally. When the gleba is colored dark above, the lower portion is still white. The trama splits, allowing the single spherical cavities to be dispersed separately after the disappearance of the peridium. This mechanism we shall see more highly developed in the Sphaerobolaceae and Nidulariaceae.

While no true stipe is formed in this family, in both genera when growing in sandy soil, the rooting base may be so highly developed as to resemble a stipe.

Lycoperdaceae.—In *Bovista nigrescens*, investigated by Rehsteiner (1892), the fructifications arise either laterally or terminally on mycelial threads. In contrast to other Gasteromycetes, its rind does not seem to continue into the peridium of the fructification, but forms only a patelliform sheath which surrounds and protects the delicate basal part of the young fungus. Furthermore, the thick, wide-lumened hyphae of the core do not continue into the core of the young fructification, but the fructification is built of thin-walled, narrow hyphae which run in the core of the rhizmorph beside the conducting hyphae.

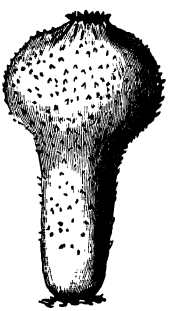
These hyphae radiate more or less distinctly toward the periphery; they are parallel and wide lumened, with clavate or flask-shaped tips, and they form the fundament of the outer peridium. Later, as in *Rhizopogon*, there are differentiated from the homogeneous core thicker and looser portions of tissue; the latter develop to cavities, the former to the knots with the outgrowing tramal pads. For a long time, from the original ground tissue at the edge of the fructification, new hyphal knots are laid down. This tissue, after fulfilling its function, grows only by the expansion of its elements and the formation of new tramal plates. By these increases in size the periphery of the ground tissue expands passively and is forced apart; its tangled hyphae become solid, arranged tangentially and form the fundament of the inner peridium.

As in some species of *Rhizopogon*, the fructifications are surrounded by tramal tissue peridium but, in contrast to *Rhizopogon*, the outer peridium is further differentiated into a radially disposed outer and a tangled inner layer consisting of slender hyphae. In time, the outer parts of this tangled zone swell up strongly and expand to a pseudoparenchymatous tissue. Consequently, the mature fructification is surrounded by four layers: the compact trama or inner peridium, the narrow zone of tangled, unthickened hyphae gradually merging with the broad pseudoparenchymatous zone which bears the outermost layer of swollen radiating cells. With increasing age, the outer layer becomes frayed and dried.

In the course of the development of the gleba from the slender tramal hyphae, there are differentiated solid, mostly aseptate branches which

gradually swell, increase their membranes and become brown. These are the future capillitium threads; their form and sculpture are important systematic characters in separating *Bovista* from related genera, as *Globaria* and *Mycenastrum*. At maturity, the peridium opens at the top, the gleba disintegrates into a dry powder which is penetrated by a tangle of capillitium.

In the cosmopolitan *Lycoperdon*, which has given this family its name, formation of the fructification takes place as in *Bovista*, only the gleba *G* is differentiated into a fertile and sterile zone (Fig. 300, *B*). Thus, as in *Bovista*, the whole interior of the fructification is constructed of a thick tissue knot covered with a hyphal palisade. In the lower columnar part of the fructification, the later stipe *st*, glebal development is retarded; the glebal chambers retain their original rounded form and the hyphal



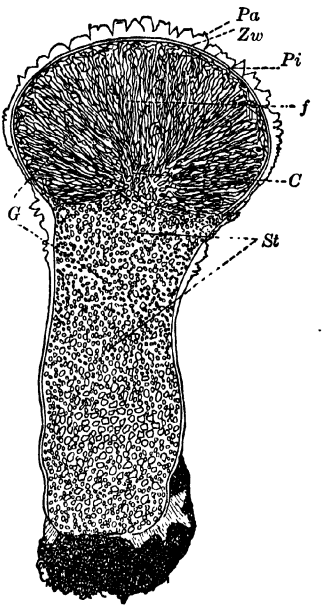


FIG. 300.—*Lycoperdon gemmatum*. *A*. Exterior of fructification (× ½). *B*. Section of young fructification (× 2). *Pa*, outer peridium; *Pi*, inner peridium; *Zw*, middle layer; *C*, rudimentary columella; *G*, gleba cavities, sterile below, fertile above; *St*, stipe. (*After Rehsteiner*, 1892, *and Strasburger's textbook*.)

palisade remains sterile. In the upper capitate part (Fig. 300 *f*), however, the cavities become compressed by rapid growth of the tramal plates, into long and narrow labyrinthine, radiating and often tortuous slits in which the hymenia deposit their spore masses. In the species with more or less cylindrical fructifications, as in *L. gemmatum*, the sterile part gradually passes over into the fertile; in the species with capitate fructifications, as *L. depressum*, there is a sharp line between the rapidly developing fertile and the retarded sterile part. This line has been formed by a horizontal pulling apart of the fertile and sterile chambers in the transition zone (Rabinowitsch, 1894). The exoperidium is

differentiated as a single layer of pseudoparenchyma, forming warts which disappear at maturity of the fructification. The endoperidium also of a single layer begins as radial, loosely-woven, thin-walled hyphae. As it matures, thick-walled hyphae, similar to the capillitium, replace the early tissue, finally forming a compact, persistent tissue. The gleba forms a number of large, subspherical primary cavities which are later cut up into numerous secondary ones by growth of the tramal plates (Cunningham, 1927).

During the maturing of the spores, the hyphae in the interior of the peridium become loose at the top of the fructification and short geniculate; the distinction between outer and inner peridium, *Pa* and *Pi*, disappears, the top is ruptured as a mouth, and the spores, penetrated by capillitium, becomes a dusty mass.

Several species of Lycoperdaceae are palatable when young, as long as the gleba is white, as *Lycoperdon gemmatum*, *Calvatia caelata* and *C. maxima*. The fructifications of the latter attain the diameter of more than half a meter. According to Buller (1909, 1924), a specimen of normal size contains 7,500 billion spores, approximately as many as 4,000 average fructifications of *Psalliota campestris*. Thus, this is the most fruitful organism known. Were these spores all to germinate and each form a fructification the size of the parent and if all the spores of these were to form fructifications, there would be produced a fungus mass 800 times the size of our planet.

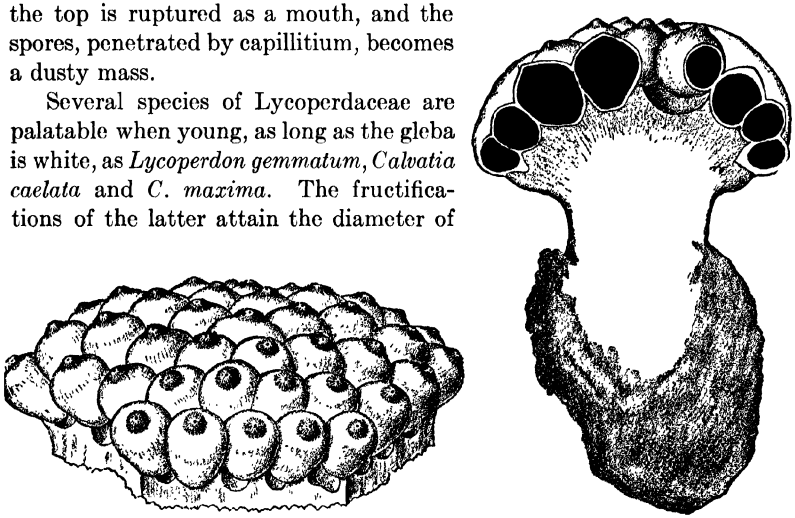


FIG. 301.—*Broomeia congregata*. *A*. Portion of stroma with fructifications. *B*. Section of stipitate stroma. (*After Berkeley and Murray.*)

In two further genera, *Diplocystis* and *Broomeia* (Fig. 301), found in South Africa and the West Indies, there are joined together on a stroma 17 by 15 cm. over 900 fructifications (Pole-Evans and Bottomley, 1918); each is surrounded by its own two-layered peridium which at maturity tears stellately at the mouth. Unfortunately, the development

of these unusual genera is unknown and hence their systematic position is still uncertain.

Throughout the family we have found an increasing differentiation of the peridium.

The fructifications of *Astraeus hygrometricus* (*A. stellatus, Geaster hygrometricus*) are hypogaeous and surrounded by mycelium. The peridium consists of a thin, papery endoperidium and a stronger exoperidium, of three layers, an outer, thin, looser, a thicker, corky, middle layer and a horny collenchyma, inner layer (Fig. 302). In both outer layers, the hyphae are irregularly intertwined. At maturity the whole gleba is disorganized and there remain only the spores with the thick-walled capillitium. The exoperidium dehisces stellately, the fructification rises above the soil. Because of the hygroscopicity of the innermost radially fibrous layer, the exoperidium curves inward in dry weather and expands

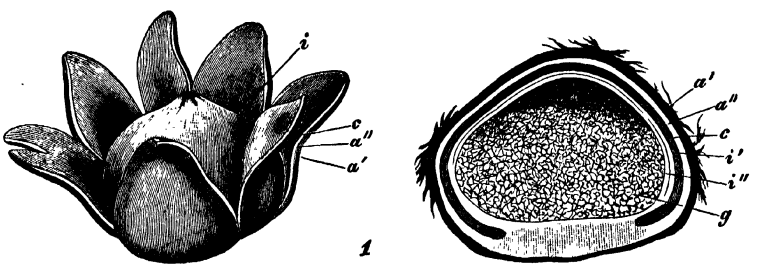


FIG. 302.—*Astraeus hygrometricus*. 1. Mature fructification. 2. Section of young fructification. *i*, *i'*, *i''*, endoperidia; *a'*, *a''*, exoperidia; *g*, gleba. (Natural size; *after Tavel and Bary.*)

in damp. The endoperidium ruptures irregularly or stellately at the top and the spores are dispersed.

In *Geaster velutinus* (Cunningham, 1927), the mycelial layer consisting of a dense palisade, 1 to 2 mm. thick of coarse, deeply colored hyphae, is first differentiated from the ground tissue. In the next stage the primordia of the fleshy and fibrillose layers of the exoperidium, the gleba and the sterile central tissue, the columella, are differentiated. The fibrillose layer consists of periclinally arranged large and small hyphae with later the addition of some hyphae similar to those of the mycelial layer. The fleshy, or inner layer of the exoperidium begins as a layer of large, compactly woven hyphae between the fibrillose layer and the gleba. The cell walls gelify and the tissue gradually becomes pseudoparenchyma. It is interrupted by the thickened base of the columella.

Shortly after the differentiation of the fleshy layer begins, a dome of cavities appears between this layer and the columella. The cavities vary in size and shape, apparently being formed by the tearing apart of the hyphae. These cavities become lined with large inflated cells, the

primary basidia, which compress the ground tissues into the tramal plates. The primary basidia arise directly from the tramal hyphae without the subhymenium characteristic of most Basidiomycetes. Meanwhile the outer portion of the ground tissue differentiates the endoperidium, which is composed of slender hyphae similar to those of the fibrillose layer. They are intricately interwoven and partially gelatinized. Differentiation of the glebal tissue is rapid, the younger basidia being much smaller than the primary basidia. Both types of basidia are typically four spored but spore numbers from one to eight are not uncommon.

A period of rapid spore production follows, until the trama is practically exhausted. Capillitium threads, hyphae similar in appearance to those of the mycelial layer, grow out from the columella.

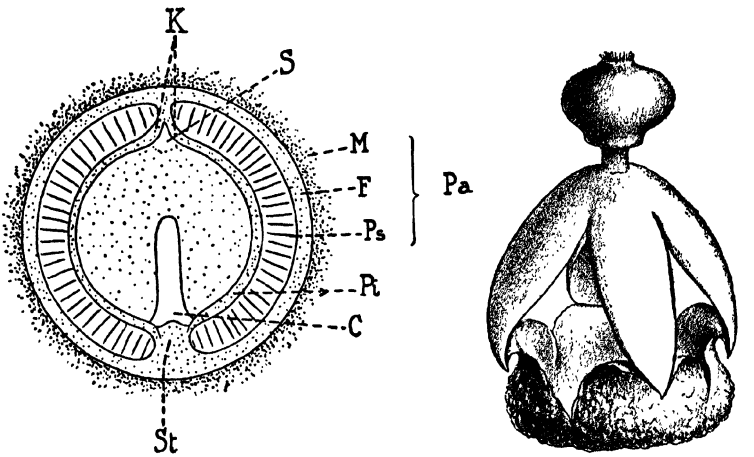


FIG. 303.—*Geaster coronatus*. *A*. Schematic section of young fructification. *Geaster marchicus*. *B*. Mature fructification. (Natural size; *after Rehsteiner*, 1892, *and E. Fischer*, 1900.)

Shortly after the endoperidium has been formed, the hyphae of the apex of the endoperidium become more loosely interwoven and form a thickened apical disc. The disc assumes a radial arrangement, a small irregular cavity appears in the center and becomes lined with hyphae from the inner portion of the endoperidium. Then the disc collapses, is depressed and gives rise to the peristome. Finally the exoperidium ruptures and exposes the endoperidium.

Differing from most other Gasteromycetes, the basidiospores, mycelium and young basidia are uninucleate. When the sterigmata develop, the nucleus divides a sufficient number of times to provide a single nucleus for each spore.

Development is essentially similar in *Geaster coronatus* (Fig. 303). First the fundament of the exoperidium is differentiated from the ground tissue,

which is only partially fertile; in the columella *C* and in the apical, conical *D*, it remains sterile. Perhaps the columella is analogous to *C* of *Lycoperdon gemmatum* (Fig. 300, *B*).

The peripheral ground tissue, which later forms the gleba, functions only a short time; long before the columella and the differentiation of the outer peridium is recognizable, it is changed into the inner peridium *Pi*. Its hyphae assume the typical periclinal direction and their membranes thicken considerably; they remain very closely intertwined, however, and form a compact membrane covering the gleba, which is interrupted only at the base and top of the fructification. At the base, its hyphae are lost into the undifferentiated stipe *St*; at the top, they loosen and thereby indicate the spot *K* where later the peristome will appear.

The outer peridium is also differentiated into three layers, a mycelial layer *M*, the fibrous layer *F*, the pseudoparenchymatous layer *Ps*. The first and third are also present in *Lycoperdon* and *Bovista*, but the fibrous layer is new. Mycelial and fibrous layers surround the whole fructification. Their connection is gradually loosened so that the former may be separated from the latter as a firm membrane; only at the top of the fructification does the connection of the two layers continue. The pseudoparenchymatous layer is not continuous but is interrupted at the base and top of the fructification where it joins with the hyphae of the inner peridium. In the remaining area, the connection with the inner peridium is lost. Whereas originally it was connected with it by a loose hyphal tissue, with increasing age its elements were more and more separated until finally, at the loosening of the pseudoparenchymatous layer, they were torn apart from the inner peridium.

At spore maturity the gleba goes through the same changes as in *Lycoperdon*. The trama disappears and only its firmer hyphae withstand disintegration as capillitium. Similarly, the more delicate elements of the sterile tramal tissue, the columella and the layers *S* swell and disintegrate, leaving only the capillitium. The hyphae of the peridium become loose at the top leaving a small opening. Their membranes thicken very markedly in the manner of the capillitium and in this species forms a cover of the peridium which is lacking in others.

Growth in breadth begins in the pseudoparenchymatous layer and the cross-section of the large, thin-walled cells doubles. The pressure thus created ruptures the peridium at the top, the point of least resistance; it splits into three layers, the mycelial layer, the fibrous and fleshy layer and the inner peridium. The mycelial layer remains, as Fig. 303, *B* shows, in the form of a subterranean, cup-like sheath whose upper third has been torn into four lobes. The earlier place of fusion of the mycelial layer and fibrous layer is retained; consequently the deeply split, fibrous and pseudoparenchymatous layer is turned inside out at the end of

the four lobes, so that the pseudoparenchymatous layer comes to lie on the convex side. By this process, the gleba which is surrounded by the inner peridium is raised above the ground. It opens, as in *Lycoperdon*, and allows its spores to scatter as dust.

The meaning of the whole apparatus is obscure. In hypogaeous forms, as in *G. coronatus*, one might consider it a means of better dissemination of spores, but in the epigaeous species this interpretation fails. Apparently none of the stipitate species have been studied intensively.

The peridium is still more developed in *Calostoma Wallisii* (*Mitremyces Wallisii*), perhaps not distinct from the common *C. cinnabarinum*

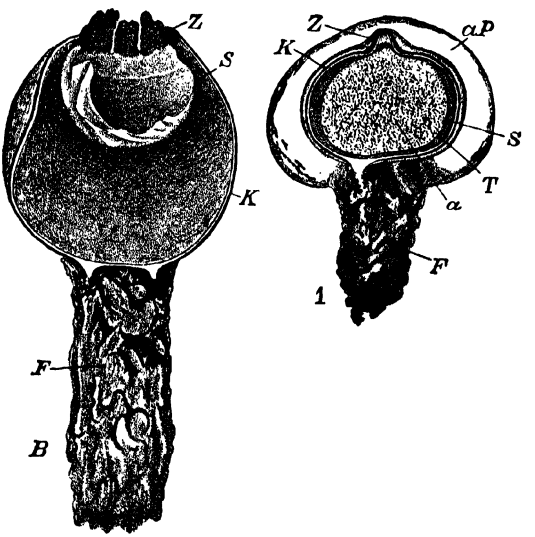


FIG. 304.—*Calostoma Wallisii*. *A*. Section of young fructification. *B*. Section of mature fructification. Explanation of letters in text. (*After Fischer*, 1884.)

(*Mitremyces lutescens*) of North America (Fig. 304). Outermost lies a thick, white, gelatinous tissue *aP*; next within follows a tough, cartilaginous, brightly colored, hollow spherical layer *K*, at whose top there is early formed a stellate, red-edged opening *Z*. In the interior lies the endoperidium *S*, which at maturity hangs from the top as a thin-walled sac. From the base of the layer *L*, as the fructification matures, there grows a stipe or rooting foot *F*, which chiefly consists of numerous, irregularly arched, cartilaginous threads which rupture the outer peridium *aP*; this stipe gradually elongates and raises the fructifications. At the approach of maturity, the layer *K* expands considerably, the layer *aP* is thereby torn, disappears and the endoperidium *S* hangs as a small sac from the mouth into the interior of the fructification and discharges

the spore powder. This genus also possesses a true capillitium (Fischer, 1884).

Astraeus and *Calostoma* are sometimes placed in the Calostomataceae in the Plectobasidiales on account of the more irregular arrangement of their basidia.

Tulostomataceae.—This family is characterized by the two-layered peridium, rind-like on the outside, papery-firm within, and the irregular gleba, penetrated by capillitium. As its development is as yet insufficiently investigated, the classification is only provisional. If the assertion of Tieghem is confirmed (see also Schroeter), that their basidia behave according to the stichobasidial type, they should be removed to the Phleogenaceae.

Tulostoma is the best-known genus, especially the cosmopolitan *T. brumale* and *T. squamosum* (*T. mammosum*) (Schroeter, 1876; Bessey, 1887;

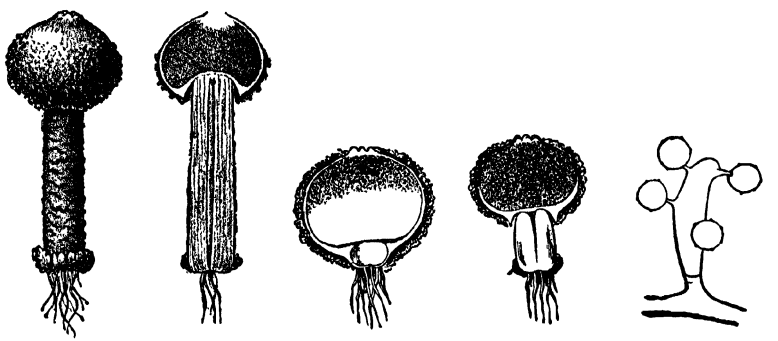


FIG. 305.—*Tulostoma squamosum*. *A*. Habit and section of fructification. *B*. Median sections of fructification before and during elongation of stipe. *C*. Basidium. (*After Vittadini and Schroeter.*)

Petri, 1904). Their fructifications appear from fall to spring and lie in the earth 2 to 3 cm. deep. They are laid down as small, sclerotial swellings of the mycelium; the rind consists of compactly intertwined, slender hyphae, the core of broad, short, inflated cells, barrel shaped in the middle, between which run at large intervals, threads of thinner, parallel-walled hyphae. The rind then differentiates into a brown crust and a firm, papery interior. The core differentiates into a middle and lower layer (Fig. 305, *B*). The core layer is approximately spherical. It is loose in texture and remains white, even through the maturation of the spores. The lower core layer is blunt, conical and consists of a cylindrical column and covering. The column is composed of parallel, slightly branched hyphae and forms the fundament of the later stipe. The covering, consisting of tangled hyphae, dries after spore maturity, leaving a small cavity between peridium and stipe at the base of the fructification.

The middle core layer appears almost reniform in cross section. It consists of a smooth tissue of slender, ramose hyphae which form club-shaped basidia at their ends.

The sterigmata are laterally inserted at unequal heights. Numerous unbranched, thick-walled, undulate hyphae, the capillitium threads, grow out from the core fibres. The basidia degenerate and only the capillitium and the ochraceous spores remain in the peridium. At maturity, the stipe elongates to 3 to 6 cm., the peridium tears at the spot where a small cavity is formed by the drying of the stipe covering (Fig. 305, *B*) and the gleba, together with the peridium, rises above the ground. During the winter the outer layer of the peridium becomes loosened with bits of earth adhering like scales, exposing the inner, lighter-colored layer (305, *A*, left) whose opening was originally closed by a solid plug, the dried upper core layer.

The stipe is still more strongly developed in the predominantly subtropical *Battarrea*, which is insufficiently known. Here it attains a length of over 20 cm. so that the fertile portion, consisting of endoperidium and gleba, projects above the ground like the pileus of a small agaric. The peridium is circumscissile, the edges roll upward and backward exposing a narrow ring of capillitium and spores. As these are carried away by the wind, the drying action of the latter cause the edges of the peridium to shrivel and roll up more, exposing more spores. This is continued until the upper half of the peridium has shriveled and blown away and there remains only a shallow cup of the lower half containing a few spores, which are finally washed away by rain.

Sphaerobolaceae.—In this family, the cosmopolitan *Sphaerobolus stellatus* has been investigated (E. Fischer, 1884; Rabinowitsch, 1894; Pillay, 1923; Walker, 1922, 1927; Walker and Andersen, 1925).

The fungus grows on rotting wood preferably. The mycelial strands are surrounded by an upper brownish (Fig. 306, *OR*) and a lower white rind (Fig. 306, *UR*) and possess a comparatively loose core. At the point where the fructification will arise, one or rarely several tissue bodies are differentiated from the core. Each of these divides into a looser ground tissue (Fig. 306, *GF*) and a firmer gelatinous rind which itself differentiates into two layers, a narrow intertwined outer and a looser inner layer (Fig. 306, *GR* and *IR*). Only in the interior of this body is the true fructification laid down as a more solid tissue (Fig. 306, *SA*) and always at the upper edges of the rind. Generally a single fructification develops in each tissue body, occasionally two.

On further growth, the fructification arches over the rind layer of the tissue body and that of the mycelial threads; when these layers disintegrate, the fructification appears above the mycelial threads (Fig. 307, 2). It is differentiated into peridium and gleba. The first is composed of four layers: the gelatinous mycelial layer *M* (which biologically corre-

sponds to the volva of the Clathraceae), the pseudoparenchyma layer *P*, a thin, tough, periclinal, fibrous layer *F*, and the collenchyma layer *C*. The outer cells of the collenchyma layer elongate radially, become prismatic and assume a peculiar palisade structure; the innermost layer next the gleba consists of large spherical cells, called cystidia by earlier writers but from their cytology probably basidia. At the top of the fructification the peridium is weaker; there it is chiefly composed of isodiametric lls.

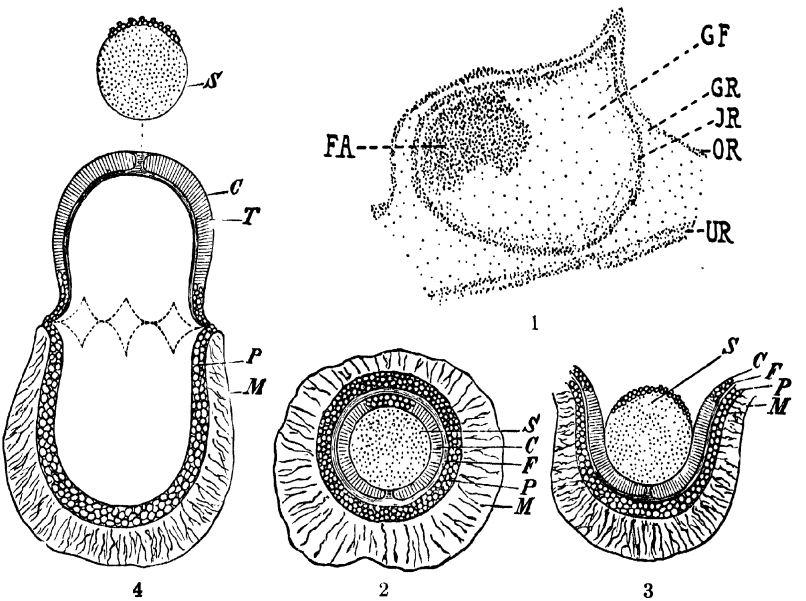


FIG. 306.—*Sphaerobolus stellatus*. 1. Median section of young hyphal strand with fundament of fructification. OR, outer rind; UR, under rind; GR, rind layer of tissue knot; JR, inner rind of gel; GF, ground tissue of tissue knot; FA, fundament of fructification. 2–4. Diagrams showing structure of fructification and discharge of gleba. (1 *after Pillay*, 1923; 2–4 *after E. Fischer*, 1884.)

The gleba *S* develops rapidly. The nine-spored basidia, which soon disintegrate, are formed in regular nests so that by the time the collenchyma has differentiated, they have collapsed. Further, the hyphae, which form the trama collapse and the gleba becomes a slimy mass in which are imbedded the spores, and gemmae. In youth the spores are uninucleate but soon become binucleate.

At maturity the isodiametric zone of the collenchyma layer splits periclinally, so that the gleba, surrounded by the inner and the proximal portion of the collenchyma, separates from the remaining peridium. Because of the stronger surface growth of the collenchyma layer, this splits, tears stellately at the top and slowly bends outwards, exposing the

spherical gleba. The collenchyma layer continues its growth, so that a strong tension exists between it and the fibrous layer. This is increased by the hydrolysis of the glycogen in the collenchyma layer to maltose and by a consequent increase of osmotic pressure. Thereupon the fibrous layer *F* separates from the pseudoparenchymatous layer *P* and turns inside out, with the attached collenchyma, quickly and forcibly (at times with a small report) ejecting the gleba *S* over 4 m. high (the size of the fructification is a few millimeters!). Occasionally the process is so forcible that the reversed part is thrown off. The gleba that has been shot off germinates as a whole by putting forth numerous germ tubes which largely develop from the gemmae, not from the basidiospores. The gemmae are capable of germination for at least seven years.

In *S. iowensis*, development is similar to *S. stellatus* (Walker, 1927). The secondary basidia by mutual pressure produce a chambered gleba with well organized hymenia. The chambers early become filled with spores. The palisade layer and the pseudoparenchyma next the gleba is interrupted by strands of conducting tissue which connect the inner and outer portions of the fructification. This species lacks the gelatinous layer in the peridium.

Nidulariaceae.—The members of this family are characterized by gleba chambers formed only in small numbers, surrounded by a special sclerenchymatous wall and hence disseminated as a unit. The tendency for the trama to split (which we found in *Rhizopogon luteolus* and in *Pisolithus*) culminates in this family.

In the forms so far studied, *Crucibulum vulgare* (Sachs, 1855), *Cyathus olla* (*C. fasicularis*) (Walker, 1920) and *Nidularia pisiformis* (Fries, 1910), the fructifications arise epigaeously on rotten wood as small knobs of tissue (*Cyathus olla* may also be cultivated on artificial media). At the periphery, the hyphae intertwine to a solid brown layer covered with hair-like hyphae. This layer, the outer peridium *ap*, subsequently assumes a corky consistency. On its interior, the light inner peridium *ip* is differentiated by a predominantly peripheral arrangement of the hyphae and a gelatinization of the hyphal walls.

Shortly after the appearance of the inner peridium, the gleba chambers are laid down in the ground tissue, and in *Crucibulum* (Fig. 307) and *Cyathus* from the bases of the fructification toward the top, in *Nidularia* in the apical part of the fructification only, while the basal part becomes lacunose and its hyphae gelify. The formation of glebal chambers proceeds in such a way that at any spot in the ground tissue the young basidia, gradually increasing in number, grow toward the common center where their ends come in contact. By the growth of the basidial layer and by the enlargement of their surfaces, the basidial tips are pushed apart so that in the chamber fundament is formed a

central cavity which constantly enlarges. This is filled by a gel which probably results from the disintegration of vegetative hyphae. The originally spherical chambers become lenticular, whereby the thicker wall tissue is formed first on the flat side, while the curved, narrow sides remain connected with the ground tissue. By secondary alterations, the wall tissue attains a very complicated structure and, in *N. pisiformis* for example, is composed of not less than five layers. Outermost there is a thin, hyaline, hyphal layer with gelatinous walls, then a brown layer

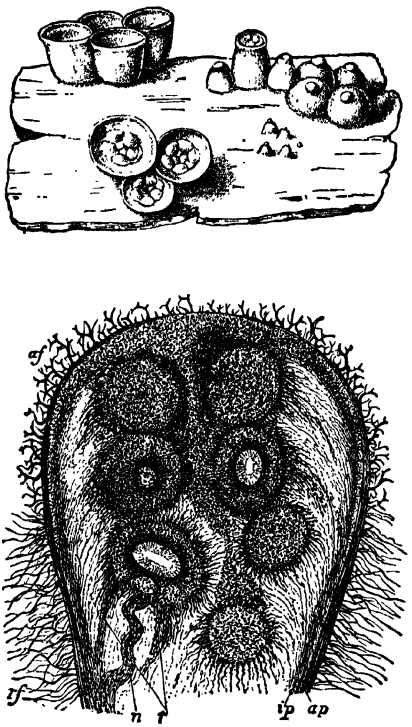


FIG. 307.—*Crucibulum vulgare*. *A*. Habit, young and mature opened fructifications. *B*. Section of young fructification showing peridioles. (*After Sachs*, 1855.)

formed of slender, compact, thin-walled hyphae, then a thin sheath of dark brown, much-thickened, coarse strands, then a true, strong, lacunose wall tissue, formed of thin-walled, brown hyphae and, finally, a pseudoparenchymatous layer upon which rests the hymenium. The basidia are four spored; the diploid nucleus divides twice (Fig. 309); in the basidium it begins a third division which is only completed in the spore, hence, as far as known, the spores are binucleate from youth. The basidia degenerate, the spores absorb the gel in the glebal cavity, fall off

the sterigmata, collect in the cavity of the glebal chamber, fill it and are further nourished by vegetative hyphae which grow out of the subhymenium, surround the spore, fuse with it and nourish it as in *Scleroderma* (G. W. Martin, 1927).

The ground tissue outside of the gleba chambers gelatinizes; in *Crucibulum* and *Cyathus*, however, on the side of each chamber next the cup wall, a funiculus attaches the chamber to the peridium. In *Cyathus* especially, it is a very complicated structure; in *C. striatus*, it consists

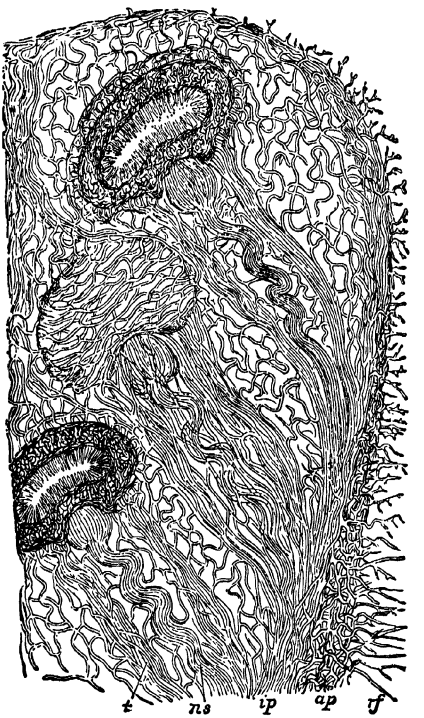


FIG. 308.—*Crucibulum vulgare.* Portion of fructification somewhat older than that shown in Fig. 307, *B*. (*After Sachs*, 1855.)

of a cylindrical basal portion, a thin middle section, and an upper portion. This is a hollow pocket which is penetrated by a funiculus fastened above to the glebal chamber and below coiled into a knot. In damp weather the funiculus may become 12 cm. long. Perhaps it aids dissemination by fastening the chambers to animals.

At maturity, the fructification degenerates at the top which, in *Cyathus* and *Crucibulum*, is a sharply defined circular cap (epiphragm). The gelatinous ground tissue liquefies and hard round gleba chambers lie,

like eggs, at the base of the fructification. These have the unfortunate name "peridioles." They do not open by themselves and the spores are only freed by injury or by decay of the hard wall. At high temperatures they germinate to strong, binucleate, clamp mycelia, which break up into oidia under certain conditions of nutrition.

In the Nidulariaceae, a part of the fructification, the peridiole assumes the task of propagation instead of the basidiospores, which, on account of their angiocarpous formation, are no longer shot away, and which, surrounded by a gel, are set free very late. Thus the biological effect of the functional degeneration of the basidia is partially compensated.

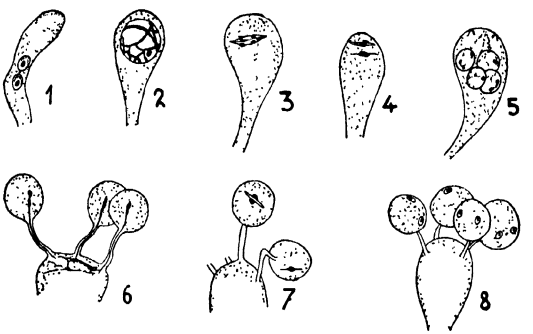


FIG. 309.—*Nidularia pisiformis*. Development of basidia. (× 1,200; *after R. E. Fries*, 1911.)

Hydnangiaceae.—In this family we return to the stage of *Leucogaster* of the Rhizopogonaceae. Here the echinulate spores are no longer imbedded in a gel and the hymenium is always compact. The first member of this series is *Hydnangium* in which we find the beginnings of several divergent lines within the family. The ontogeny of this large genus has been little studied. The majority of species have a simple peridium, not greatly differentiated from the texture of the trama. Apparently as a degeneration phenomenon, we have a series of light-spored species with progressively thinner peridia, until finally the peridium is absent in some Californian species, as *Gymnomyces Gardneri* and *G. Stillingeri*. In the opposite direction we get a gradual thickening of the peridium and darkening of the spores, reaching a climax in *Hydnangium Fitzpatrickii*, with nearly black spores and a thick peridium of pseudoparenchyma.

A still higher group of species has the peridium differentiated into two layers and nearly black spores, typified by *H. citrinum*. Such data as are available, lead one to believe that the cavities form in a hemispherical dome just under the peridium and develop basipetally until the whole glebal tissue is filled with cavities. The immature condition of a number

of species was misinterpreted and at one time the name *Octavinia* was applied to them, incorrectly since it was originally used as a synonym of *Melanogaster*.

In some species, as *Hydnangium pusillum*, there remains a hemispherical base of sterile tissue which is prolonged below into a short stipe, reminiscent of conditions in *Jaczewskia* and *Hymenogaster Behrii*.

Perhaps a continuation of this tendency is found in the poorly known *Lycogalopsis*, the only genus of the family which is not found in or on the ground. In the Javan *L. Solmsii* (E. Fischer, 1886), the fructifications are 4 to 5 mm. in diameter (Fig. 310, *a*) and occur on the fruits of *Parinarium scabrum*. The fundaments appear as inverted patelliform portions of hyphal tissue, in which thick, concentric layers, tapering at the edge,



FIG. 310.—*Lycogalopsis Solmsii*. *A*. Habit (natural size). *B*. Vertical section of immature fructification. (× 26; *after E. Fischer*, 1886.)

are separated by loose layers; apparently the layering results from periodic unequal growth, as in the formation of annual rings. When the gleba is formed, a peripheral tissue, which may include one or more layers, becomes grayish and develops to a peridium (Fig. 310, *b*). In one of the inner layers, rapid intercalary growth occurs, forming a hemisphere. Within, a hyphal palisade develops along with the glebal chambers in an unknown manner. At maturity, this degenerates, the peridium shrinks and a few remains of the tramal plates jut into the cavity, forming a rudimentary capillitium.

Returning to *Hydnangium*, in *H. sociale*, a caespitose species in California, we frequently have a partial fusion of fructifications. In section, therefore, we frequently find deeply penetrating layers of peridial tissue, closely resembling sections of *Protubera* in appearance. This should probably be interpreted, however, as a convergence phenomenon rather than an indication of phylogenetic relationships.

In *Hydnangium carneum*, which alone has been cytologically investigated (Ruhland, 1901; Petri, 1902; Bambeke, 1904), there are extensive irregularities in the development of the basidium, which sometimes forms only one spore, into which occasionally all four nuclei migrate. As far as is known, an early division occurs in the normally developing spores, as is usual in most Gasteromycetes.

Stephanospora carotaecolor differs from *Hydnangium* only in having a conspicuous collar at the base of the basidiospore.

In an unidentified species, tentatively placed in *Hydnangium* by E. Fischer (1925), development is gymnocarpous at first and similar to that in *Elasmomyces*, but eventually the columella is obliterated by the formation of new cavities suggestive of those in *Chamonixia* and *Gallacea*.

In *Arcangeliella*, a columella penetrates the gleba branching into tramal plates, as in *Elasmomyces*, but distinguished from it by the presence of latex ducts similar to those of *Lactarius*, and by slightly different spore markings. In *A. caudata*, the peridium is thin, with the outer hyphae perpendicular to the surface of the fructification. The cells of these hyphae break apart easily as oidia, but it is unknown whether they are capable of germination (Zeller and C. W. Dodge, 1919). In the cosmopolitan *Arcangeliella Stephensii* (*Hydnangium Stephensii*) E. Fischer (1925) reports the development similar to that of *Elasmomyces*. In *A. violacea* (*Hymenogaster violaceus*) the peridium becomes viscid, as in some species of *Hymenogaster*, and the spores are more ellipsoidal.

The highest member of the series is *Maccagna*, where the tramal plates are differentiated into two kinds: the thick primary branches of the forked columella, composed of varicose hyphae and abundant latex ducts, and the secondary branches of tramal tissue composed of slender, compact hyphae without latex. Neither *M. carnica* nor *M. tasmanica* has been studied carefully, but the structure of the mature plant is suggestive of conditions we shall meet again in *Phallogaster*.

The main line of development proceeds through *Elasmomyces*, which lacks the latex organs of the *Arcangeliella—Maccagna* series. In *Elasmomyces krjukowensis* (*Secotium krjukowense*) the fructifications are developed gymnocarpously (Bucholtz, 1901); the columella is percurrent and continuous with the peridium at the top. The peridium (pileus, of some authors) rolls in toward the bottom without being connected to the stipe; a few of its hyphae, however, may intertwine with the stipe hyphae, but the line between the two tissues may be easily recognized. Both peridium and stipe are composed of strands of slender hyphae and nests of pseudoparenchyma similar to the structures found in the Lactariaceae.

The tramal plates grow further from the pileus toward the interior of the cavity, intertwine at their tips with hyphae from the columella and form numerous folds which anastomose with each other. This

results in a confused mass of chambers, whose cavities were originally connected and open at the base of the pileus. At maturity, the peridium cracks off, allowing the basidiospores to be disseminated.

This line culminates in *Macowanites*, where some of the larger Californian species, still undescribed, reach a height of 7 cm. with a flat, agaricoid cap 14 cm. in diameter. These larger forms are suggestive of the higher Agaricales and were it not for the large number of intermediate forms in this series, would be placed in that order, as Conard (1915) and Gäumann (1926) are inclined to do in the case of *Endoptychum*.

Hymenogasteraceae.—This family is characterized by the colored, fusiform to citriform spores, and closely parallels the Hydnangiaceae in many respects. We may look for its origin in forms like *Melanogaster* of the Rhizopogonaceae. The first stage is represented by *Hysterogaster*, with deep yellow, smooth, fusiform spores, somewhat similar in shape to those of *Hysterangium*. Its ontogeny is not well known, but the gleba is filled with labyrinthiform cavities at maturity, as in *Rhizopogon*. The peridium is somewhat differentiated from the trama and the septa are said to be somewhat thicker in the center than next the peridium in *H. luteus* (*Hymenogaster luteus*), but there is no trace of a columella (E. Fischer, 1927). The details of the formation of tramal plates and cavities was not studied. The peridium of *H. fusisporum* (*Hymenogaster Barnardi*) is less well developed.

The large, central genus of this family is *Hymenogaster*, corresponding to *Hydnangium* of the Hydnangiaceae. Here we have an assemblage of species which ontogenetic investigations will probably show to belong to several series, if not to different genera. The spores are usually citriform, yellow to brown, and often variously roughened.

In an unidentified species which Fischer (1927) places in the group of *H. lilacinus* or of *H. populetorum*, probably in the former if my interpretation of his figures of immature specimens is correct, cavities form in a dome-shaped area under the pseudoparenchymatous(?) peridium and gradually develop basipetally. Growth is centrifugal from the central ground tissue. If this method of development should be found typical, it might explain a large section of the genus where the basal portion of the fructification remains sterile until quite late in its development, such as we find in the *H. tener* group (Fig. 311, *A* to *C*). In *H. Behrii* this tissue remains as a highly differentiated hemispherical basal portion from which thick septa radiate toward the peridium, as we have seen in *Hydnangium pusillum* and *Lycogalopsis* and shall see again in *Jaczewskia*. In *Hymenogaster fragilis* this base is prolonged into a stipe below, suggesting *Lycoperdon* in appearance.

In *Dendrogaster* we have a persistent columella. Perhaps the most primitive species is *D. candidus*, where the sterile base is prominent and the columella relatively small. The peridium is pseudoparenchymatous

and thin, while the septa are thick and composed of slender tramal hyphae. The spores are small, ellipsoidal and minutely verrucose. In an unnamed California species, the columella penetrates only about half way through the fructification, and is but slightly branched, while the septa are much

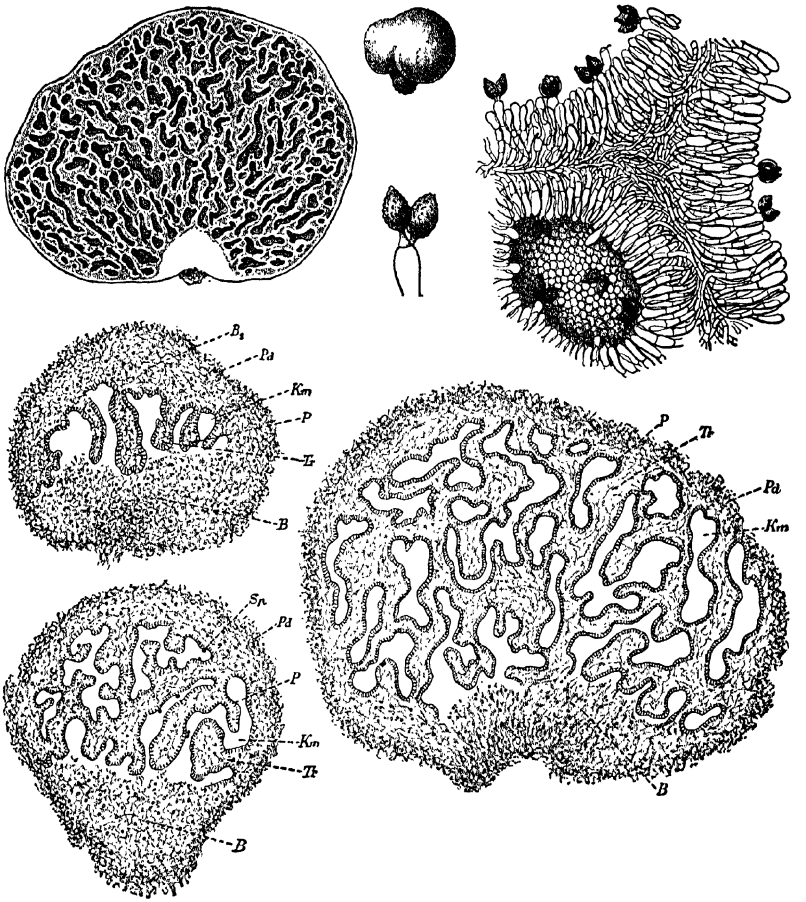


FIG. 311.—*Hymenogaster tener*. *A*. Habit (natural size). *B*. Section of fructification (× 3.5.) *C*. Portion of gleba. (× 120.) *D*. Basidium and spores. (× 450.) *After Tulasne*.) *Hymenogaster Rehsteineri*. *E* to *G*. Sections showing development of fructification. (× 450; *after Rehsteiner*.)

thinner and the spores much larger. In *D. cambodgensis*, the peridium is distinguished by fascicles of erect yellow hyphae. In the other subgenus, marked by a gelatinous sheath about the spore and a disappearance of the sterile base, we get a gradual development of the columella from *D*.

utriculatus, where it penetrates the center of the fructification, and, in an undescribed species from Tennessee, ends in a spherical knob from which the septa radiate. In forms like *D. globosus* (*Hymenogaster globosus*), it is dichotomously branched and nearly percurrent, as in the *Elasmomyces* group of the Hydnangiaceae. The spores in this species are longitudinally ribbed suggesting *Gautieria* where the spores are characterized by 8 to 10 longitudinal ribs.

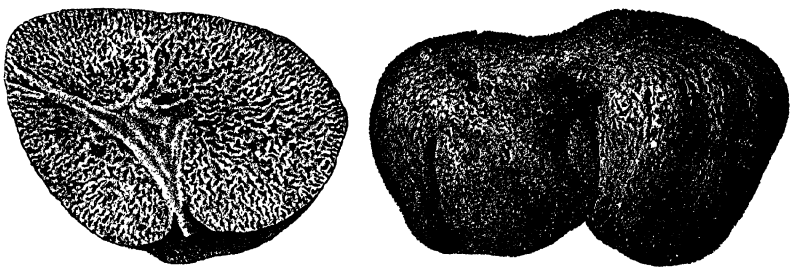


FIG. 312.—*Gautieria graveolens*. *A*. Habit. *B*. Section of fructification, showing columella and tramal plates. (× 2; *after E. Fischer*, 1900.)

In *Gautieria* we have a gradual degeneration of the peridium from such species as *G. Rodwayi* and *G. Parksiana* with thick peridia, through undescribed species with thin evanescent peridia, to species where the peridium is absent at maturity, although still present in young individuals. Only this last group has been studied ontogenetically (Fitzpatrick, 1913). The fructifications are spherical, furrowed and 0.5 to 2.5 cm. or more in

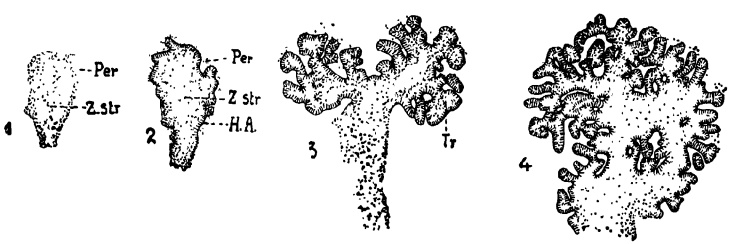


FIG. 313.—*Gautieria graveolens*. Development of fructification. *Per*, peridium; *z. str*, columella; *H. A.*, hymenial fundament; *Tr*, tramal plate. (*After Fitzpatrick*, 1913.)

diameter (Fig. 312). They develop from clavate ends of rhizomorphs. The rind consists of loosely interwoven inflated hyphae, incrusted with calcium oxalate; it continues unaltered into the peridium of the young fructification (Fig. 313, 1). Similarly, the core of the rhizomorph becomes the columella of the young fructification. Its hyphae are intermingled somewhat with swollen hyphae, and run parallel to the axis. In the peripheral parts, they radiate toward the peridium and form dense

palisades (Fig. 313, 2, *H*, *A*). Further development proceeds from these palisades. The subhymenial tissue grows outward, forming tramal plates which anastomose freely and form the cavities of the gleba, lined with the developing hymenium. The peridium is pushed outward by the growth of the gleba, and since growth ceases early, the hyphae are torn apart and gradually disappear, leaving the glebal cavities exposed at maturity, as in *Gymnomyces*. As the tramal plates grow out from the central strand it gradually collapses and forms a cartilaginous forked columella. At maturity, the fructifications give off a pungent odor which attracts rodents and thus secure dissemination. In *Gautieria plumbea* the columella is much more highly developed, being nearly percurrent and having broad primary branches, as well as a slender stipe.

The end member of this series is apparently *Chamonixia caespitosa* (*Hymenogaster caerulescens*, if the synonymy given by Fischer (1925) is correct). The fructifications at first develop gymnocarpously, then the peridial hyphae unite with the stipe. Finally the columella disappears as its sterile tissue is completely differentiated into gleba. The original figures of Rolland rather suggest a coalescence of caespitose fructifications such as we have found in *Hydnangium sociale*.

Two anomalous species which perhaps should be transferred to form a new genus, *Hymenogaster verrucosus* and *H. Rehsteineri*, occur in eastern Europe. In young individuals (Fig. 311) the peridium *Pd* consists of closely interwoven hyphae surrounding a loosely tangled ground tissue *BB*, and the fundament of the gleba. The tramal plates grow downward from the upper part of the peridium into the glebal chamber *Km*, like the lamellae of the Agaricales. The tramal plates branch, anastomose forming the glebal cavities and finally fuse with the ground tissue at the base (Fig. 311, *G*.). The mature fructification has the same structure as that of the *H. lilacinus*(?) group, which has a different ontogeny. At present there is no way of knowing which method is followed by the greater number of species.

Hysterangiaceae.—In this family we again return to the Rhizopogonaceae. A primitive (or reduced?) form, *Gallacea Scleroderma* resembles *Rhizopogon* at maturity and is sometimes classified in that genus (*e.g.*, Zeller and Dodge, 1918, under *Rhizopogon violaceus*). The fructification first appears as a pyriform branch of a rhizomorph (Cunningham, 1924). A dome-shaped zone in the outer portion of the glebal primordium cuts off the future peridium, composed of compact, ramose hyphae, the outer portion, of which is violet in color. The first cavities are few and large. The secondary cavities are successively differentiated from the columella tissue or formed by the rapid growth of tramal plates into the large primary cavities, eventually cutting them up into a large number of small ones. Cavities are also formed from the inner portion of the peridium, as in *Rhizopogon*. When the columella, which here acts as a ground

and nurse tissue, has all been used up, the whole gleba gelifies and forms a thin, collapsed lining of the peridium, leaving a large, empty space in the middle. The mycelium is wholly binucleate. As usual, fusion of the dicaryon occurs in the basidium. The fusion nucleus forms six nuclei which migrate into the spores and divide once, producing binucleate basidiospores.

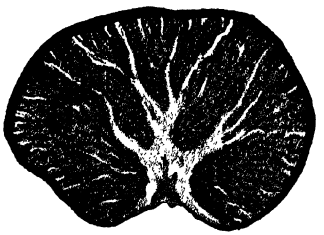


FIG. 314.—*Hysterangium clathroides*. Section of mature fructification. (× 2; *after E. Fischer*, 1900.)

In *Jaczewskia*, a rare genus found once in Russia and once in British Columbia, the fructification consists of a gleba supported on a large sterile base which is slightly prolonged below into a short stipe. Several primary tramal plates grow upward from this base and give rise to the anastomosing secondary tramal plates (Mattirolo, 1912; C. W. Dodge unpublished observations).

In *Hysterangium* the well-developed columella is persistent to maturity. In *H. nephriticum* the sterile base is prominent and persistent, with the columella scarcely more than a branch rising from it. As we saw in *Dendrogaster*, the columella becomes increasingly well developed as the sterile base disappears. *H. inflatum* is also reminiscent of *Dendrogaster*,

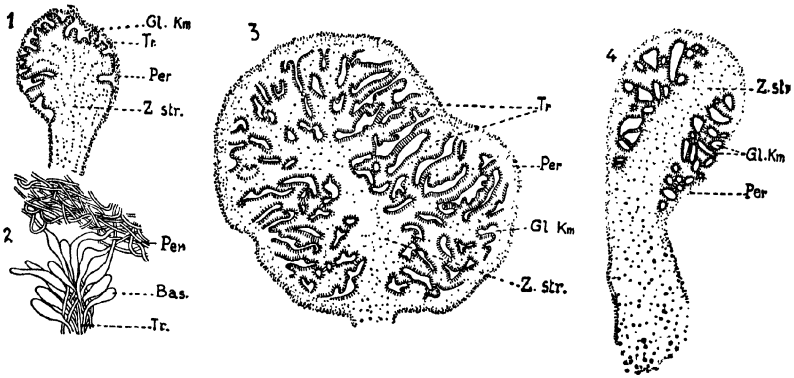


FIG. 315.—*Hysterangium clathroides*. 1, 3. Median sections of young fructifications. 2. Section of periphery of young fructification. (1 × 10; 2 × 7; 3 × 270; *after Rehsteiner*, 1892.) *Rhopalogaster transversarium*. 4. Diagrammatic section of young fructification. *Gl. Km*, gleba cavities; *Tr*, tramal plates; *Per*, peridium; *Z. str*, columella; *Bas*, basidial fundaments. (× 10; *after Johnston*, 1903.)

with its inflated, gelatinous sheath about the spore. In this group, the peridium, although of different texture from that of the trama, is homogeneous and composed of slender parallel hyphae. From forms like these, there is a series to those with a highly developed columella and a peridium of coarse, thick-walled hyphae, and, finally, a well-developed pseudo-

parenchyma, such as we find in *Hysterangium clathroides* (*H. stoloniferum* var. *americanum*), the only species to be reported upon ontogenetically (Rehsteiner, 1892; Fitzpatrick, 1913). In this species, the tramal plates arise from the columella and anstomose in all directions (Fig. 315, 1 and 3). Where the hyphal palisade borders the glebal cavities it forms a hymenium. The ends of the tramal plates next the peridium fuse with it (Fig. 315, 2). At the proximal side of this zone, the tramal hyphae may pierce the palisade in a tangential direction and approach the peridium laterally. In this species the bulk of the peridium is composed of pseudoparenchyma.

In an undescribed species from California, the columella is very thick and the ends of the tramal plates rarely reach the peridium, leaving a single large cavity lined with a hymenium. The columella suggest a pine cone projecting into the cavity. In another undescribed species from the same region, the columella ends in a spherical knob in the center of the fructification, from which radiate the primary tramal plates.

From this point, the columella is percurrent and develops along two diverging lines, one main line with the tramal plates continuing to develop from the columella, the other with the tramal plates developing increasingly from the top of the columella and the adjacent peridium, suggesting the Agaricales in both ontogeny and final product. In this latter line, which we will discuss first, the tramal plates disappear at maturity, leaving the spores as a powdery mass within the dry peridium, as in *Endoptychum* and *Podaxis*. The main line continues through *Rhopalogaster* and *Phallogaster* to the Clathraceae and perhaps the Phallaceae.

In *Secotium* we have the counterpart of *Elasmomyces* and *Macowanites* in the Hydnangiaceae. In fact these genera, along with several other poorly known genera, are often included in a separate family, the Secotiaceae. Conard (1915) and Gäumann (1926) regard this group as an aberrant member of the Agaricales, modified by its hypogaeous habitat. On the other hand, Lohwag (1924, 1927) and Cunningham (1925), following the traditional viewpoint, consider this group as a family of the Gasteromycetes, forming the culmination of the Hymenogastraceous line. *Secotium* is confined to S. Africa, Australia, New Zealand and the west coasts of South and North America. The fructifications are fleshy and firm and the gleba is never fragile and powdery, as in *Endoptychum* and *Podaxis*.

Both *Secotium erythrocephalum* and *S. Novae-Zelandiae* have been studied ontogenetically (Cunningham, 1925), the latter in most detail. Although most of the species of this genus are hypogaeous or epigaeous, both these species are found on decaying wood in New Zealand. The plants are gregarious, enabling one to find many developmental stages on a single piece of wood. The first stage shows a furrow separating the stipe

fundament from that of the pileus, such as we find in the gymnocarpous Agaricales. The fundament of peridium and gleba shows a deeply staining ring containing a small radial lacuna, below which is a cuneate ring of loosely woven hyphae, the primordium of the partial veil. The lacuna, which extends as a ring around the base of the columella, enlarges and the hyphae lining its roof arrange their tips in a palisade which gradually covers the whole cavity except its floor. The tramal plates grow downward from the top of the cavity until they meet and anastomose with the walls of the cavity, dividing the large cavities into smaller ones, such as we have seen in *Gallacea Scleroderma*, and somewhat resembling the growth of the lamellae or tubes in the higher Agaricales. At the same time, other cavities are formed in the undifferentiated gleba above the original cavity, corresponding to those formed from the inner portion of the peridium in *Gallacea*, but different from any structures reported in the Agaricales. About the time basidia appear in the palisades of the cavities, the peridium is differentiated and as the pileus expands, the furrow between it and the columella widens and deepens. The partial veil makes little growth after it is differentiated, and hence is torn apart and disappears at maturity. A few remnants persist about the stipe, giving it a fibrillose appearance similar to that of the cortina in mature species of *Cortinarius*. The columella pushes gradually up into the developing ground tissue of the pileus, just ahead of the formation of cavities, reaching and merging with the peridium when the fructification is about half grown.

S. erythrocephalum agrees with this development in most particulars. Its peridium is more highly differentiated, becoming covered with a definite gelatinous layer, filled with pigment granules which originally lined the walls of the cells. In material collected by Zeyher at Uitenhage, South Africa, and determined as *S. Gueinzii*, Berkeley (1843) reports a well-developed volva which persists as polygonal areoles in mature specimens. The spores are also said to be similar to those of *Hymenogaster albus*, rather than the ellipsoidal, smooth or asperate spores of other species of *Secotium*. Cytologically, the life cycle is the same as in *Gallacea*, all portions being binucleate, with fusion of the dicaryon and meiosis in the basidium and a mitosis in the young basidiospores.

Endoptychum, similar to *Secotium* and often included in that genus, is confined to the drier regions of the north temperate zone. The only well-known species is *E. agaricoides* (*Secotium agaricoides*, *S. acuminatum?*), with a purely angiocarpous development similar to that of *Secotium* (Conard, 1915; Lohwag, 1924*a*). The youngest fundaments of the fructification form a homogeneous body of tissue, surrounded by a firm peridium. A closed annular hymenial cavity is developed within the tissue. By increased local growth of certain subhymenial tissues, lamellae with cystidia grow toward the stipe and columella. On account of the

limited space, these lie in numerous folds and finally fuse with the hyphae of the stipe. At maturity the peridium breaks or is loosened from the stipe at its lower margin and expands, as in some species of *Secotium* and *Macowanites*.

As a last member of this series we may mention *Podaxis carcinomalis* (*Podaxon carcinomale*) with much the same geographical distribution as *Endoptychum*, being confined to the warmer, drier regions. The fructifications consist of a solid woody stipe and columella, a fusiform glebal tissue and a fragile, scaly peridium (Fig. 316) which separates from the top of the columella and from the stipe, and cracks longitudinally around the lower edge. The gleba is spongy with the tramal plates reduced to strands of hyphae bearing tufts of basidia. Maturation proceeds from below upwards, the gleba eventually forming a dusty mass of capillitium and spores, as in the Lycoperdaceae; Gäumann (1926) places it in a separate family as an appendix to the Agaricales, emphasizing its similarity to *Endoptychum* (*Secotium*) which he also placed in this order.

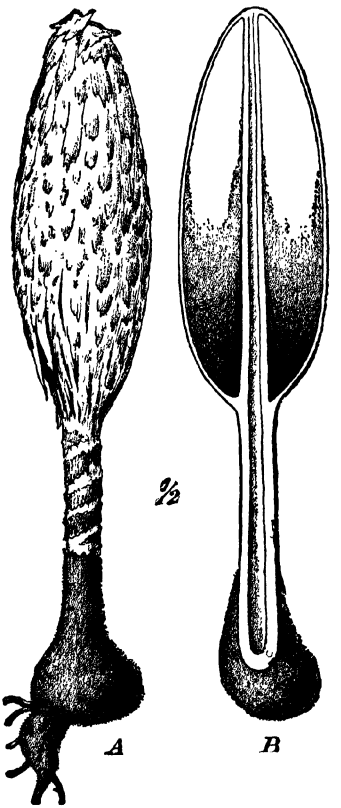


FIG. 316.—*Podaxis carcinomalis*. *A*. Exterior. *B*. Section of fructification. (× ½; *after Schweinfurth*.)

The main line of the family, leading toward the Clathraceae, develops from forms similar to *Hysterangium fuscum* (*H. Gardneri*), but having a completely percurrent columella and a more highly developed stipe. The small spores and the more or less gelatinous consistency is retained.

Rhopalogaster transversarium (*Cauloglossum transversarium*) of the southeastern United States, continues this tendency. The shape of the mature fructification is similar to that of *Podaxis* (*Cauloglossum*), in which group it was formerly placed, or still more like that of *Clavaria pistillaris* (Johnston, 1902). The primordium of the gleba is first seen as a ring of small chambers surrounding the upper third of the club. The tissue outside this ring, the fundament of the peridium, which consists of loosely interwoven hyphae, ceases growth and is gradually stretched by the developing gleba until it becomes thin and torn

in many places, very much as we have seen in *Gautieria graveolens.* As the gleba develops, the tramal plates bend and anastomose, forming cavities similar to those of *Rhizopogon,* which the gleba resembles in general appearance (Fig. 315, 4).

Phallogaster continues this tendency with more highly developed tramal plates. *P. saccatus,* on rotten wood in North America, has been more fully studied (Thaxter, 1893; Fitzpatrick, 1913). Here the tramal plates are definitely differentiated into primary and secondary plates, the primary lacking a hymenium (Fig. 317, *A*). In longitudinal section, they appear as branches and hence are called columella branches (*st. zw*); laterally they anastomose, forming radial, polyhedral cavities, opening outward, whose tips lie at *a* on the upper surface of the colu-

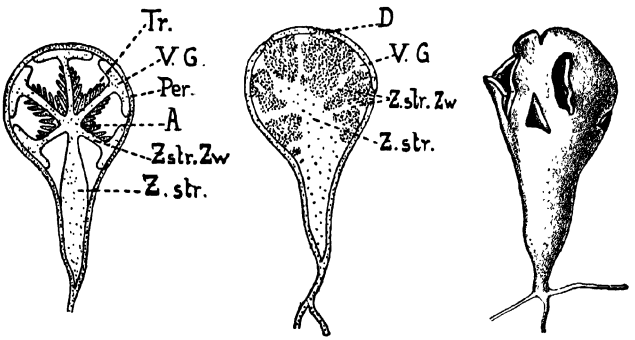


FIG. 317.—*Phallogaster saccatus. A.* Diagrammatic section of young fructification. *B.* Section of mature fructification. *C.* Habit, showing dehiscence. (Natural size; *B, C after Thaxter.*)

mella. In tangential section the walls of the cavities form a mesh. The tips of the primary branches spread out under the peridium to scutellate plates, which are called volva gel plates *Vg.* Rudiments of these structures are also present in *Hysterangium Fischeri* of California where the ends of the tramal plates broaden so much that inside the peridium they form a narrow layer, only occasionally pierced by tortuous cavities (Fischer, 1908). This layer is more or less gelatinous.

The fertile secondary plates arise from the primary plates, as in *Maccagna;* thus being retarded both in time and place of formation. They push into the polyhedral cavities and converge between the plates *VG.* In the limited space they lie in labyrinthine furrows and fuse with the neighboring plates into a very tangled group of chambers. Although the course of individual gleba chambers can no longer be followed, one must still assume that they remain open outward toward the peridium. The surface of the tramal plates is covered by a hymenium of 6- to 8-spored basidia. At the ends of the tramal plates in the gaps between

the volva gel plates *VG*, the palisade remains sterile and changes into a pseudoparenchyma.

At maturity, the secondary tramal plates and hymenium become a dark, olive-green gel containing the primary tramal plates, the columella and portions of the volva gel plates (Fig. 317, *B*, *C*). The portions of the peridium lying between the volva gel plates develop zones of dehiscence *D*, resulting in a ragged peridium through which the spores escape.

Mutatis mutandis the changes from *Hysterangium* to *Phallogaster* are parallel to the *Pachyphloeus–Piersonia* series. *Pachyphloeus* and *Tuber* would correspond to *Hysterangium*, *Piersonia* with its localization of the fundaments of the asci to the inner folds, to *Phallogaster*.

Clathraceae.—While in the previous family, the tramal plates grow into a free space which the branches of the columella create by pushing the peridium outward, in this family, they grow into an intermediate tissue which is subsequently absorbed, leaving the cavities.

In the Brazilian *Protubera Maracuja* (Moller, 1895), the youngest stages show a clavate widening of the mycelial strand, whose rind passes into the peridium and whose core becomes the gleba of the young fructification. The branches of the columella arch outward enclosing portions of peridial tissue, which is not pushed outward. This included tissue is called intermediate tissue or peridial plates, *Zw.Gefl.* (Fig. 318, 2). With increasing size of the fructification, it also grows in breadth (Fig. 318, 3). In the meantime, a centrifugal growth of the columella branches sets in, expanding it radially. Its fate is variable; in the peripheral parts it is crushed into narrow peridial plates *Zw.gefl.pl.* by the branches of the columella which there spread out to the scutelate volva gel plates *VG* (Fig. 318, 4 and 5). These peridial plates persist and separate the volva gel plates at maturity. Further toward the interior, the branches of the columella do not spread out to such a degree; here, their longitudinal growth forms an elongate cavity *Gl.Km*, which is still filled with the loose remnants of the peridial plates. These cavities, which correspond to the polyhedral glebal chambers of *Phallogaster*, are not originally developed as cavities but result from the disintegration of the intermediate tissue.

In a corner between the branches of the columella *HA*, the hyphae which radiate from these branches are arranged (even in the stage of Fig. 318, 3) in a palisade which spreads laterally and covers the walls of the cavities. As in the Hysterangiaceae and *Phallogaster*, tramal plates, which develop to the labyrinthine tangle of the mature gleba, are formed by the local growth of the tissue beneath.

The mature fructification (Fig. 318, 1) has a diameter up to 5 cm. The peridium *Per* is at most ¼ mm. thick, and consists of a brown, pseudoparenchymatous tissue. It does not contrast with the gleba, but lies upon the white or often almost bluish volva gel *VG*, 2 to 3 mm. thick which is connected through the gel-plates, the branches of the columella

Z. str. zw., with the gel mass at the base of the fructification (the earlier columella *Zstr.*). At maturity the peridium bursts open irregularly. The volva dissolves into a white slimy solution with which the greenish spore mass mingles. It has a strong odor, reminiscent of the flowers of *Passiflora alata.*

This new formation of an intermediate tissue in *Protubera* attains a full development in *Clathrus.* This may be exemplified with *C. cancella-*

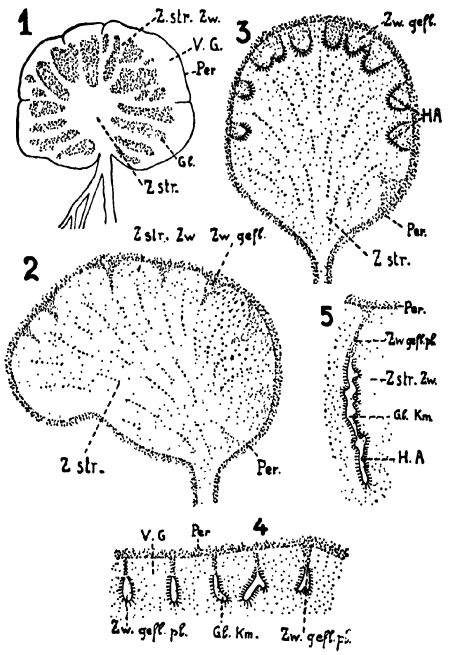


FIG. 318.—*Protubera Maracuja.* 1. Section of mature fructification. 2. Section of young fructification. 3. Advanced stage. 4, 5. Section of periphery. (1, natural size; 2 to 5 × 11; *after Möller*, 1895.)

tus (*C. ruber*[1]), found in Europe and North America, and in *C. columnatus*, in North and South America (E. Fischer, 1891, 1900; Burt, 1896). As in all the order, the fructifications develop from rhizomorphs in which the core and rind both increase in thickness. As in *Protubera*, the branches of the columella grow out of the core and spread out later to volva gel plates. In contrast to both of these, in *Clathrus* the branches of the columella are not plates but true

[1] *Clathrus ruber* is the correct name for this plant according to the International Rules of botanical nomenclature, but most authors since Persoon have preferred *C. cancellatus* [Tournef] L. ex. DC. Hence I prefer to do likewise and intend to offer this case to the next Botanical Congress for inclusion in a list of nomina conservanda.

columns. Our Figs. 319, 320 may be distinguished from the corresponding stage in *Protubera* (Fig. 318) by the smaller number of branches of the central columella and by a greater development of the separating portions of intermediate tissue: further, the separation into columella and tangled intermediate tissue spreads over the whole fructification. In the *Protubera* stage (Fig. 318, 2), the articulation of the columella is still incomplete, as the tissue indicated as such includes the whole central and basal mass of the fructification. In *Clathrus*, however, the separation continues to the base, and the columella becomes a true central axis surrounded by peripheral tissue.

As in *Protubera*, the hyphal palisade *HA*, which later expands laterally, is laid down in the corners between the branches of the columella (Fig. 319, 2), and the intermediate tissue is compressed by the developing columella branches, especially at the periphery where these branches spread out into gel plates *VG*. In the central parts, however, there remains more space for the intermediate tissue. In contrast to *Protubera* (herein lies the distinct progress over this genus), these parts of the intermediate tissue are not dissolved and there are differentiated from them, at least in *Clathrus cancellatus* (toward the hyphal palisade *HA*), a thicker hyphal knot *Rp* (the first fundament of the receptacle, which is separated from its surroundings by a loose layer of tissue. In time the peripheral hyphae become arranged in a palisade.

The strong sidewise growth of branches of the columella is very marked (Fig. 319, 3); in section, the parts *VG* represent polygonal areas which are continued by the narrow plates of intermediate tissue and separated from one another, but are beginning to gelify.

Further, especially in the upper portions of *HA*, the columella branches elongate radially, whereby the hyphal knot *Rp* is pushed away from the palisade *HA*, and shoved outward so that a cavity arises between *Rp* and *HA*. This cavity is surrounded by a hyphal palisade, the lateral continuation of the original palisade, and is the first glebal chamber *Gl. Km.* In the distal side of the first hyphal knot *Rp*, in *C. cancellatus*, further knots are separated from each other and their surroundings by a narrow layer of loose tissue, the separation being most complete in the older inner knots, less complete in the outer.

By the radial elongation of the columella branches, the gleba chambers increase in size (Fig. 319, 4). Meanwhile individual portions of the wall of the branch of the columella, covered by the hymenial palisade, arch over in ridges, elongate, increase in number, branch and eventually form the labyrinth of cavities and tramal plates which characterizes the gleba of the Gasteromycetes. In the distal parts of the gleba, where this touches the intermediate tissue, the hyphae of this tissue grow into the glebal chambers, fill them, hinder the change of the palisade to hymenium and intertwine repeatedly to a pseudoparenchyma. Similarly, the palisades

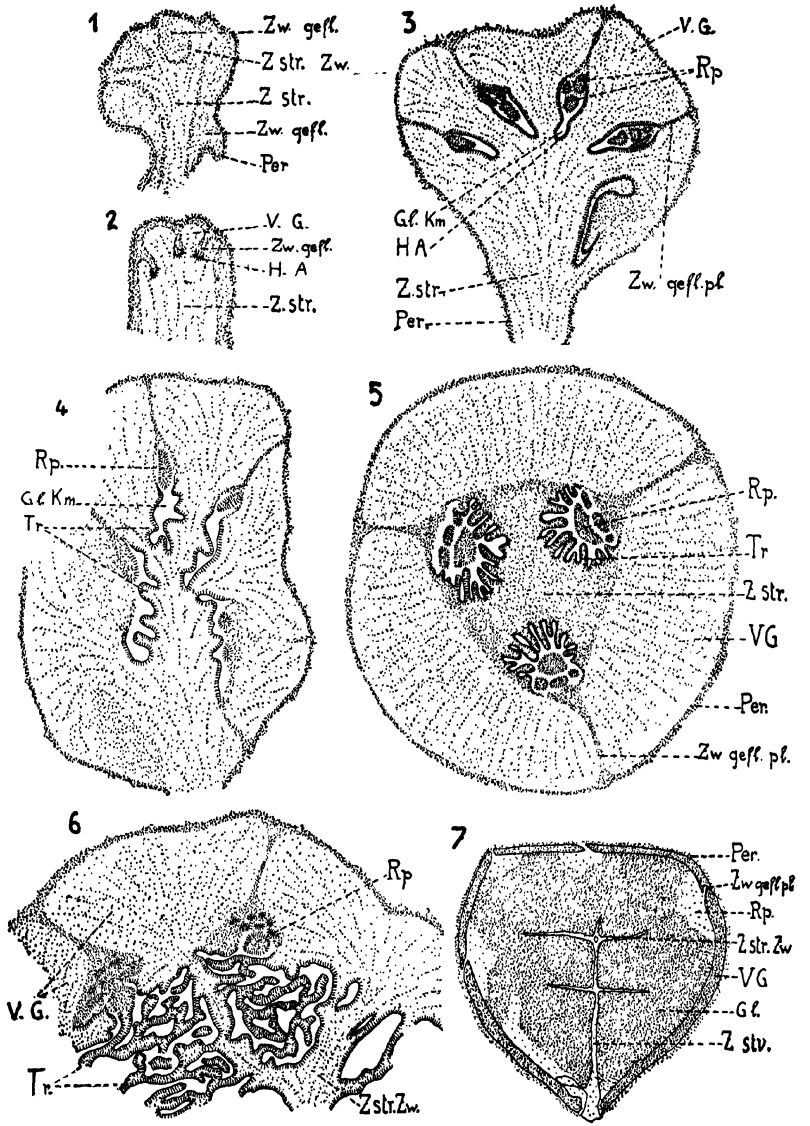


FIG. 319.—*Clathrus cancellatus*. 1. Median section of very young fructification. *Per*, peridium; *z. str*, columella; *Zstr. zw.*, branches of columella; *Zw. gefl.*, intermediate tissue; 2. Older stage. *H.a.*, palisade fundaments; *Rp*, receptacle knot; *V.G.*, volva gel plate; 3. Differentiation of knot of *Rp.*, older stage; *Gl. Km.*, glebal cavities; *Zw. gefl. pl.*, plates of intermediate tissue; *Tr.*, tramal plates. 4. Columella and branches with tramal plates. 5. Diagram of young fructification. 6. Section of mature fructification. 7. Section of young egg where the gleba has begun to turn green. (1 to 6 × 18; 7 × 2; *after Fischer*, 1891.)

which in *C. cancellatus* surround the knot *Rp*, change into pseudoparenchymatous tissue. This collective pseudoparenchyma later gives rise to the receptacle walls. In *C. columnatus*, they arise singly from the hyphae of the intermediate tissue which eventually grow luxuriantly between the peripheral tramal plates; in *C. cancellatus* independent hyphal knots, which already have been differentiated in the intermediate tissue, participate in the formation of the receptacle walls. On account of the close contact which is formed by the growth of the hyphae of the intermediate tissue into the peripheral glebal parts, the gleba remains suspended after elongation of the receptacle.

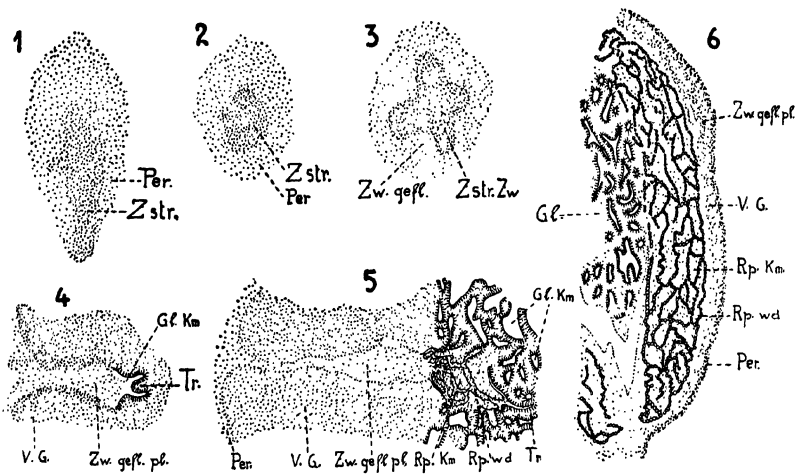


FIG. 320.—*Clathrus columnatus*. 1. Vertical section of fundaments of a fructification. 2. Horizontal section. 3. Same, older stage. 4. Older stage, showing fundaments of first glebal cavities and tramal plates. 5. Older stage. Intermediate tissue has grown into the peripheral chambers forming pseudoparenchyma, *Rp. wd.* 6. Longitudinal section of mature egg at beginning of elongation of receptacle. Letters as in 317, except *Rp. Km.* receptacle chambers; *Rp. wd.*, wall of receptacle chambers. (1 to 4 × 30; 5 × 17; 6 × 3; *after Burt*, 1896.)

Toward the end of the development, the hymenial palisade changes to hymenia of eight-spored basidia. The parts of the intermediate tissue and gleba surrounded by the receptacle walls gelify, so that receptacle cavities result.

Figure 319, 7 is a medial cross-section through a so-called egg, *i.e.*, an immature fructification shortly before expansion. The axis of the greenish gleba *Gl*, occupying the greater part of the space, is penetrated by the columella which soon swells. The rays which proceed from it are the branches of the columella. On account of their tortuous course they cannot be followed to the volva in a section; furthermore, in contrast to *Hysterangium*, they are very thin in comparison to the gleba and

inconspicuous. Around the gleba are found volva plates *VG* separated from each other by parts of the intermediate tissue (*Zw. gefl. pl.*). Within the volva, there are transverse or oblique branches of the receptacle *Rp*; its pseudoparenchymatous walls grow unusually strong and, because of lack of space, lie in thick folds: as the receptacle branches spring from the same tissue as parts of the intermediate tissue, in Fig. 319, 7 the cross sections of receptacle branches always lie inside the plates of intermediate tissue.



FIG. 321.—*Clathrus cancellatus*. Expanded receptacle. (*After Fayod.*)

The result of the development is shown in Fig. 321. While all mature fructifications of the Hysterangiaceae appear tuberiform, the Clathraceae show a marked change. The folds of the receptacle branches elongate at maturity, because of an increase of turgor, rupture both rind tissue and volva and elevate the gleba from the sheath of these two layers. The gleba liquefies, drops away and the basidiospores are spread, possibly by wind or insects. Finally, there remains only the receptacle whose form for *C. cancellatus* is shown in Fig. 321. In *C. columnatus*, the branches do not form a lattice but they resemble the ribs of a dome.

In the Brazilian *Blumenavia rhacodes* (Fig. 322), in the curve between the branches of the columella, one trama plate Tr_1 is formed earlier or is better developed than the others (Möller, 1895; E. Fischer, 1900). This elongates until its ends press against the receptacle fundament *Rp*, spreads out here and surrounds the fundament with a bifurcation. While in further development, the hymenium normally is formed on the proximal part of these plates, there arises on the distal bifurcations *R* in direct continuation of this hymenium, a pseudoparenchymatous layer *Ps*; the tissue *R*, surrounded by the pseudoparenchyma *Ps*, thereafter behaves as a receptacle chamber and is organically united with the remaining receptacle chambers.

Hence on the outside of ripe fructifications (Fig. 322, 3) lies the rind layer *Per*, which surrounds the volva gel plates *VG*. These are connected with the columella *Zstr.* by its branches *Z. str. zw.* Between the volva gel

plates lies the torn portion of the intermediate *Zw. gefl. pl.* whose proximal end extends into the receptacle branches *Rp.* In cross section, these form the outline of an acute sector with the base outward and the sides closely connected with the gleba *Gl.* The apex continues through the plate Tr_1 to the columella. In contrast to *Clathrus cancellatus*, the central branches do not anastomose with one another but, like those of *C. columnatus*, rise from the base to the top of the fructification like the ribs of a dome.

In the unfolding of the fructification, the plates of the intermediate tissue, the branches of the columella, the tramal plates Tr_1 and the tissue *R* gelify; the peridium and the volva gel burst, and the receptacle rises out

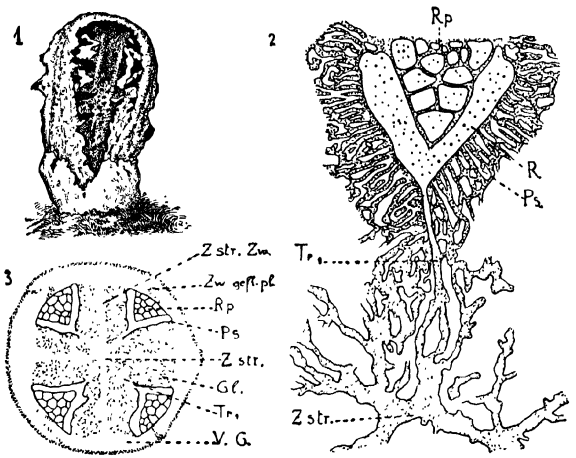


FIG. 322.—*Blumenavia rhacodes.* 1. Mature fructification. 2. Section of receptacle branch of immature fructification. 3. Section of immature egg. (1 × ½; 2 × 8; 3, natural size; *after Möller*, 1895, *and E. Fischer*, 1900.)

of it with a rapidity of up to 1 mm. per minute. As the eight columnar gleba portions are only connected with the receptacle columns, they are shifted outward through the papery aliform layer *Ps*, and exposed to the air from the interior of the lantern. The layer *Ps*, however, is not able to follow the stretching of the receptacle branches; it tears to pieces and remains hanging from the margins of the orange-yellow receptacle branches as bizarre rags, carrying on their exterior the dirty green gleba which soon drops away.

In the Brazilian *Clathrella chrysomycelina*, during the earlier stages, a rind layer *Rd* is differentiated about the columella (Fig. 323, 1; Möller, 1895; E. Fischer, 1900, 1910). This follows the branches of the columella (which, here in contrast to *Clathrus* and like *Hysterangium*, are plates and not columns) and surrounds it even when these ends have spread to the

volva gel plates (Fig. 323, 3). This gelified rind *Rd* also surrounds the parts of the intermediate tissue, in the form of horns whose points lie in the angles between the branches of the columella. As in *C. cancellatus*, the

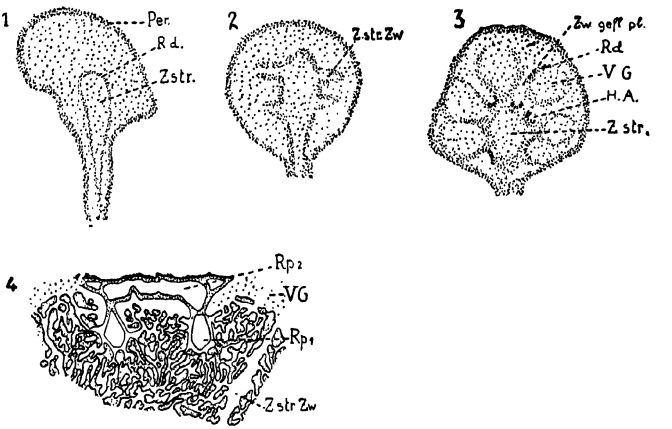


FIG. 323.—*Clathrella chrysomycelina.* 1. Section of young fundament of fructification. 2. Beginnings of columella branches. 3. Later stage showing fundament of hyphal palisade. 4. Part of section of an almost mature egg. (1 to 3 × 15; 4 × 30; *after Möller*, 1895.)

tramal plate is formed in these angles and (in the intermediate tissue) the receptacle chambers; in contrast to *C. cancellatus* (Fig. 319), however, the tramal plates are not irregularly arranged but grow up on the inmost, oldest receptacle chambers and surround them on three sides, (Fig. 323, 4, Rp_1) whereby they intertwine closely with the pseudoparenchyma of the chamber wall. The receptacle chambers Rp_2, which later are formed further out, do not come into contact with the first receptacle chamber Rp_1. They do not come into close contact with the tramal plates, however, but remain separated from them by a layer of gelatinous hyphae. Therefore, the gleba in the mature expanded receptacle does not hang as a whole (as in *C. cancellatus*) from the interior of the receptacle branches but only in small portions, surrounded by the torn *Rd* in the corners of the nets in small knobs, the original receptacle chambers Rp_1 (Fig. 324). It is further characteristic of *Clathrella*, that at its base the latticed branches fuse to a tube. The receptacle, thus, no longer rises in these lower parts, corresponding to the splits in the branches of the columella, in the form of single columns but as a hollow cylinder around the columella.

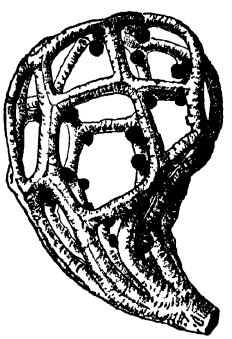


FIG. 324.—*Clathrella chrysomycelina.* Unfolded receptacle. (× ⅘; *after Möller*, 1895.)

This formation of a basal tube leads from *Clathrella* to a series of other genera whose receptacle extends into a longer or shorter stipe, as *Simblum* (Fig. 325) and *Colus* (Fig. 326). Both may be considered as stipitate *Clathrus* or *Clathrella* forms, but with the gleba confined to the apical portion of the receptacle (Conard, 1913).

In contrast to these forms is the Chinese *Lysurus Mokusin*, where the distal parts of the branches of the columella, not the proximal, show intercalary growth (Fig. 327, *D*). The receptacle fundament *Rp* remains lying in the curve of the branches of the columella *pl* and the originally narrow cavities *Gl. Km.* do not arise, as in *Clathrus* (Fig. 319), between *Rp* and *HA*, but on both the exterior, distal sides of *Rp*. As the receptacle lies directly on the columella, there is no space there for the development of the tramal plates; these grow rather from sides of the branches of the columella *Pl* into the free space outside the receptacle, so that the gleba finally lies between the receptacle *Rp* and the volva gel plates *G*, and consequently clings to the un-

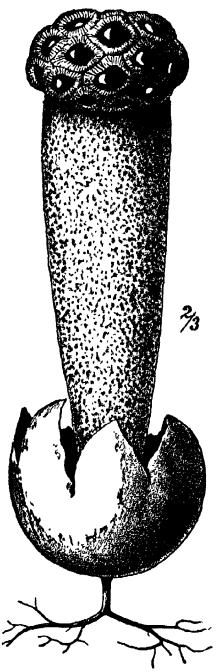


FIG. 325.—*Simblum sphaerocephalum* (*S. rubescens*) Mature specimen. (× ⅔; *after Gerard.*)



FIG. 326.—*Colus Garciae.* Mature fructification (Natural size; *after Möller*, 1895.)

folded fructification (as will be discussed in the Phallaceae) on the other side of the receptacle branches.

A development probably similar to that of *Lysurus*, is that of the South African *Kalchbrennera corallocephala* (*K. Tuckii*) whose ontogeny is incompletely known (Fig. 328). A pallid stipe, cylindrical or thicker toward the top, rises from the volva. At the clavate tip, the stipe wall disappears into a narrow-meshed lattice whose ribs (the continuation of the stipe wall) are colored an intense cinnabar red and are a cross-wrinkled above. Up to this point the receptacle corresponds to that of

Simblum. Here, there rise from the lattice bars toward the outside, cinnabar red and cross-wrinkled processes which, however, generally end free but occasionally do anastomose at their ends with neighboring processes. These ends are often broadened into two short aliform proc-

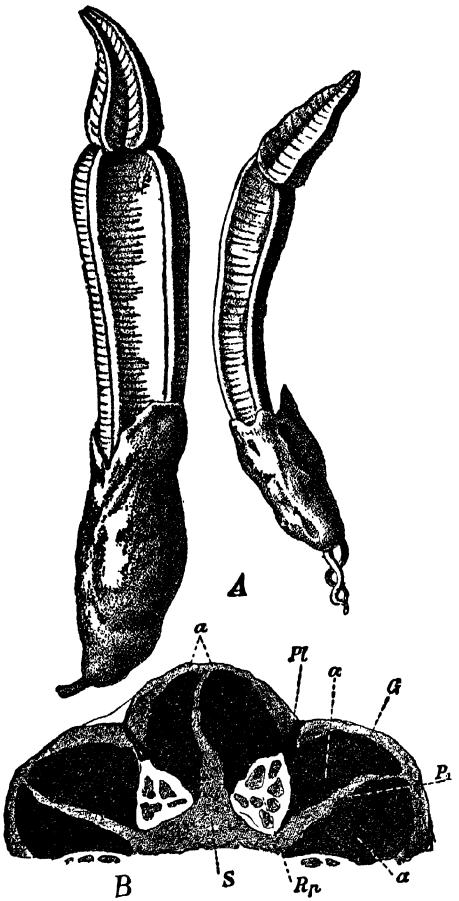


FIG. 327.—*Lysurus Mokusin.* *A*. Habit of mature fructification. *B*. Section of the upper portion of young fructification. *A*, gleba; *Pl*, plates of intermediate tissue; *G*, volva gel; P_1 branch of columella; R_p, receptacle; *S*, columella. (*A*, natural size; *B* × 4; *after Cibot and E. Fischer*, 1893.)

esses. Generally a process corresponds to every mesh of the lattice and bends obliquely over its mesh. On the processes and between them, traces of dark spore masses still remain (E. Fischer, 1891).

As in *Lysurus*, the gleba develops toward the exterior of the receptacle lattice; thus the tramal plates proceed in all directions from the columella,

as in *Clathrus*. On the fourth side, the columella branches differentiate new hyphal knots *rp*, which are surrounded later by receptacle chamber walls and connect with the remaining lattice receptacle further inwards. The parts of the receptacle in question lie directly along the whole length of the columella branches and form the thorn-like processes.

Anthurus, leading from *Colus Garciae*, has receptacle branches which no longer anastomose at the top and hence, in mature specimens, surround the gleba from below like the fingers of an open hand. Figure 329 shows this for *Anthurus Sanctae-Catharinae*, which has not been studied

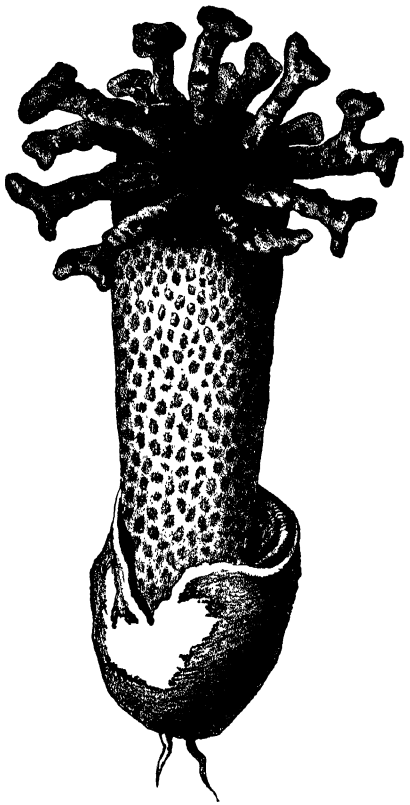


FIG. 328.—*Kalchbrennera corallocephala*. Mature individual. (Nearly natural size; *after Kalchbrenner*.)

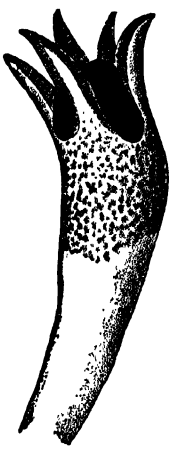


FIG. 329.—*Anthurus Sanctae-Catharinae*. Mature individual showing gleba. (Natural size; *after E. Fischer*.)

ontogenetically though a related form *A. borealis* (*Aysurus borealis*) (Burt, 1894) has been thoroughly investigated.

The polymorphous *Aseroe*, which is closely related to *Anthurus*, will be discussed more thoroughly on account of its relationship to the next family. In *Aseroe arachnoidea* (Penzig, 1899; E. Fischer, 1910) the ground plan of the fructification is similar in principle to that of *Clathrus*. From the columella *Z. str.*, there proceed (Fig. 330, 1) the vertical plates *Z. str. zw.* (branches of the columella) which later divide the gleba into a corresponding number of similar vertical flabella with the alternate plates

of intermediate tissue *Zw. gefl. Pl.* and the fundaments of the receptacle branches *Rp.* The plates of intermediate tissue, however, no longer extend to the rind of the upper part of the fructification but end blindly. The corresponding young stages have not yet been investigated, but

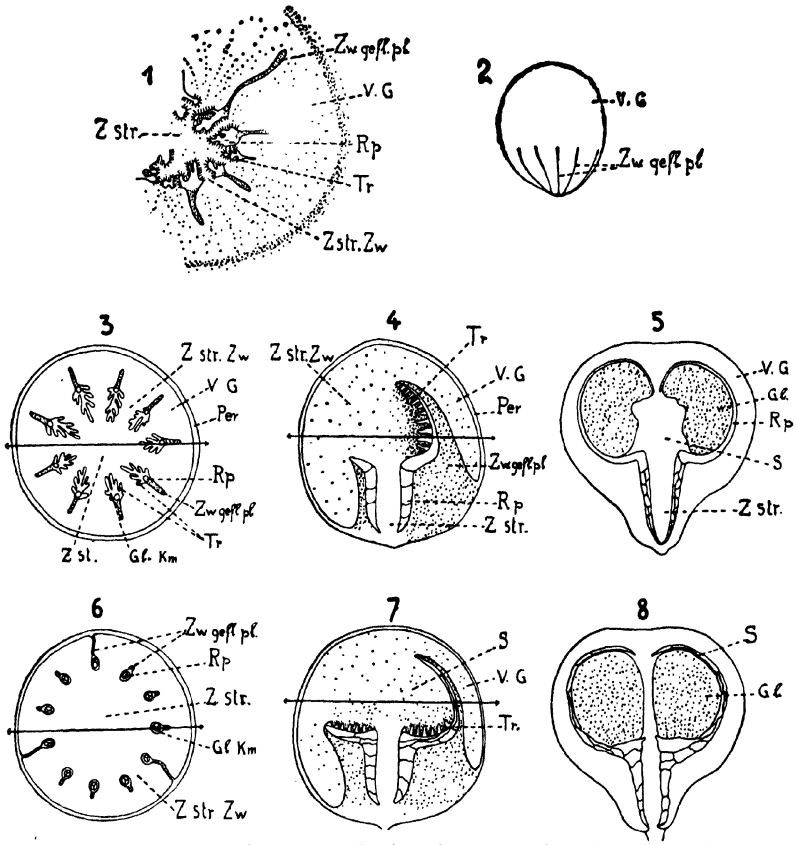


FIG. 330.—*Aseroë arachnoidea.* 1. Section of upper portion of young fructification, where the formation of the first tramal plates has begun (× 13). 2. Diagram of egg after removal of rind tissue. 3. Diagrammatic section of a portion of a fructification in the direction of the arrow in 4. 4. Section of fructification in the direction of the arrow in 3. At the right, a branch of the receptacle in median section, at the left a branch of the columella. 5. Median section of immature fructification. *Aseroë rubra.* 6. Diagram of upper portion of fructification in the direction of the arrow in 7. 7. Diagram in the direction of arrow in 6. 8. Median section of immature fructification. (*After E. Fischer,* 1910.)

perhaps this results because the loose intermediate tissue in the upper part of the fructification loosens from the rind tissue and is pushed inwards by the swelling volva gel plates; thus in the upper part of the fructification the separate volva gel plates fuse into a continuous cover.

Near the base of the fructification, plates of intermediate tissue remain in contact with the rind and, as in *Clathrus*, extend from the columella to the surface (in Fig. 330, 2 the rind tissue is removed and the volva gel laid bare): the volva gel *VG*, adhering above, splits below into a number of lobes corresponding in number to the receptacle arms. The lobes which separate the *Zw. gefl. pl.* continue as meridional pads through the interior of the fructification to the top.

As in the other Clathraceae, tramal plates *Tr.* proceed from the branches of the columella; they converge more or less toward the receptacle arms and intertwine with the pseudoparenchyma. Figure 330, 3 gives a cross section through the upper part of a young fructification. Outside is the continuous volva gel layer *VG* which continues inward to the branches of the columella *Z. str. zw.* into the columella *Zstr.* Between the branches of the columella there lie the cavities *Gl. Km.* into which grow the tramal plates *Tr.* converging in the direction of the receptacle arms *Rp.* Figure 330, 4 gives a cross section in the direction of the arrow in Fig. 330, 3. From the inside, the top of the tramal plates *Tr* push against the receptacle branch *Rp* and lie next it. As a peculiarity of *Aseroe*, these tramal plates arise only on the sides of the branches of the columella but not on their lower edge. This lower basal edge spreads horizontally, remains in contact with the receptacle fundament and divides, in the formation of a pseudoparenchyma, the "margin" of the stipe wall. It is characteristic of *A. arachnoidea* that the receptacle branches elongate considerably and grow from above, bending over into the gelatinous columella *Z. str.*

One can best conceive the whole arrangement of a young *Aseroe* fructification by comparing the volva *VG* with the pileus of a young *Coprinus* whose edge reaches the base of the fructification and splits into several lobes. The columella would then correspond to the stipe, and the vertical, plate-like branches would be comparable to the lamellae. A marked difference lies in the new tissues which form the trama, and which grow out from branches of the columella and fill up the spaces between "lamellae." Thus, in a mature fructification, the gleba occurs between the lamellae in the proximal zone, the receptacle branches in the distal. Less marked but distinctive for the appearance of the fructification is the fact that the "pileus" (volva) is ruptured at the top, the "stipe" (columella) and the "lamellae" (columella branches) dissolve, and only the considerably enlarged receptacle expands and spreads out the gleba on its arms.

In *Aseroe rubra* (E. Fischer, 1893, 1910; Bernard, 1908) still more modifications of the plates of intermediate tissue and of the trama occur. As here also no young stage has been investigated adequately, we must rely on schematic reconstructions (Fig. 330, 6 and 7). In contrast to *A. arachnoidea*, the plates of intermediate tissue no longer fuse

with the outer part of the fructification. It is always possible, however, that a few of them, as indicated in the scheme, are more strongly developed and extend to the rind. Similarly, the narrow cavity *Gl.Km.*, together with the tramal plates which converge toward the receptacle branches, is only slightly developed or has almost disappeared; only the receptacle branches remain.

Along with this degeneration, the fundaments of the tramal plate have undergone an important change. They no longer arise on the vertical sides of the columella *Z. str.* and the branches of the columella (in cross section invisible, Fig. 330, 6), but only on the underside of the columella which is swollen capitatively over the mouth of the stipe, out of the columella *Z. str.*, as well as from the capitate end *S* and from the volva.

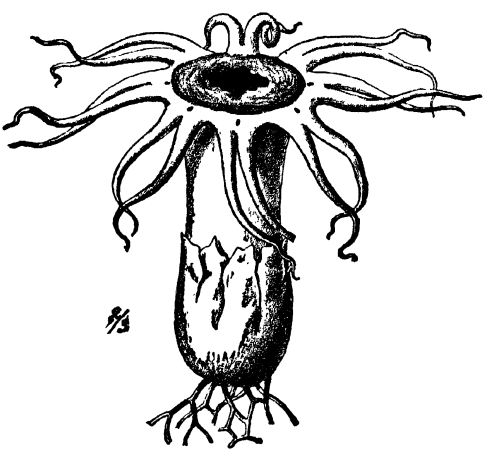


FIG. 331.—*Aseroë rubra*. Mature fructification after the disappearance of the gleba. (× ⅔; *after Berkeley.*)

Hence they cannot converge toward the branches of receptacle but run downwards toward the disciform margin which surrounds the stipe mouth and fuses with it. As the tramal mass can only expand upward in its further development, the gel *S* is pushed toward the top and the receptacle branches. It covers the gleba thinly, thereby preventing the tramal plates from becoming connected with the receptacle branches, as in *A. arachnoidea*. In the mature fructification the spore mass only clings firmly to the horizontal disc, about the mouth of the stipe. In contrast to *A. arachnoidea* the receptacle arms no longer bear a spore mass (Fig. 331). Thus, the older portion of the receptacle has lost its original function as support of the gleba.

Thus the Clathraceae show three stages of development. In the first stage, as *Protubera*, there arise sterile plates or branches of the columella

which grow out into the interstices created by the columella branches, and filled by intermediate tissue. On the distal ends, the columella branches spread into scutiform structures, the volva gel plates, which surround the interior of the fructification like an endoperidium. In the second stage, which begins with *Clathrus* and *Clathrella* and extends to *Anthurus*, there arises in this intermediate tissue a new organ, the receptacle, which comes into close connection with the gleba, raises it from the ground and from the sheath of the volva and the peridium and makes possible an entomophilous dissemination. In the lower forms, as in *Clathrus*, the receptacle is everywhere in contact with the gleba. In the higher forms, there is differentiated an increasingly insignificant apical part which serves as the point of attachment of the gleba and a basal part, always increasing in importance, which fulfills the true mechanical function of the receptacle. In the highest forms of the third stage, in *Aseroe rubra*, the apical part the connection between receptacle and gleba becomes lost, the gleba lies on the top of the columnar receptacle stipe and is raised up by it. The vestiges of the earlier receptacle branches which bore the gleba are functionless, the plates of intermediate tissue are degenerate and in the egg stage the fructification is completely surrounded by the volva gel. If one now imagines the receptacle branches are entirely degenerated, so that only receptacle stipe remains, one has the forms which will be discussed in the following family.

Phallaceae.—The organization of the fructification of the Phallaceae shows great similarity to that of the Clathraceae; as in the latter, there is formed a receptacle, a gleba and a volva. Similarly, the ripe fructifications of many species, as in the higher Clathraceae, emit an offensive, penetrating odor which attracts insects. The Phallaceae, however, differ from the Clathraceae in many details.

As in the Clathraceae, the fructifications of *Mutinus* arise as terminal swellings of rhizomorphs, whose core (Fig. 332, 1) passes over into the columella *Z. str.*, and whose rind becomes the loose rind *R* of the young fructification. At the top of the columella the hyphae radiate to a sheaf-like head *K* (E. Fischer, 1887, 1891, 1895, 1900, 1922, 1923; Moeller, 1895; Burt, 1896; Petch, 1926).

Most of the subsequent development takes place in this head. It swells much, forces the rind apart and is differentiated (Fig. 332, 2) into a loose layer *VG*, which soon gelifies, and to a closely intertwined central portion *O*, where the differentiation of the columella continues (Fig. 332, 3), dividing into an axial gelatinous column *Z. str.* and to a cap *AP* which surrounds the top of the elongated columella. The cap is differentiated (Fig. 332, 4) into the loose intermediate tissue *A* and more solid peripheral zone *P*. On the inner proximal side of the zone *P*, there arises as a cylindrical cover, a hyphal palisade *H.A.*, which arches over in pads and forms the fundament of the future gleba.

Only a portion of the following stage can be shown at once since in the meantime the fructification has grown too large. Such a section is given in Fig. 332, 5, where the rind and the volva gel *Vg* are separated. The differentiation of the columella proceeds through the cap *P* to the volva gel. Similarly the stipe *St* of the fructification has elongated; subsequently its bulk increases still further and soon exceeds the sporiferous part. Along the columella *Z. str.* there has been differentiated from tissue *A*, a thicker chambered cover, the fundament of the future

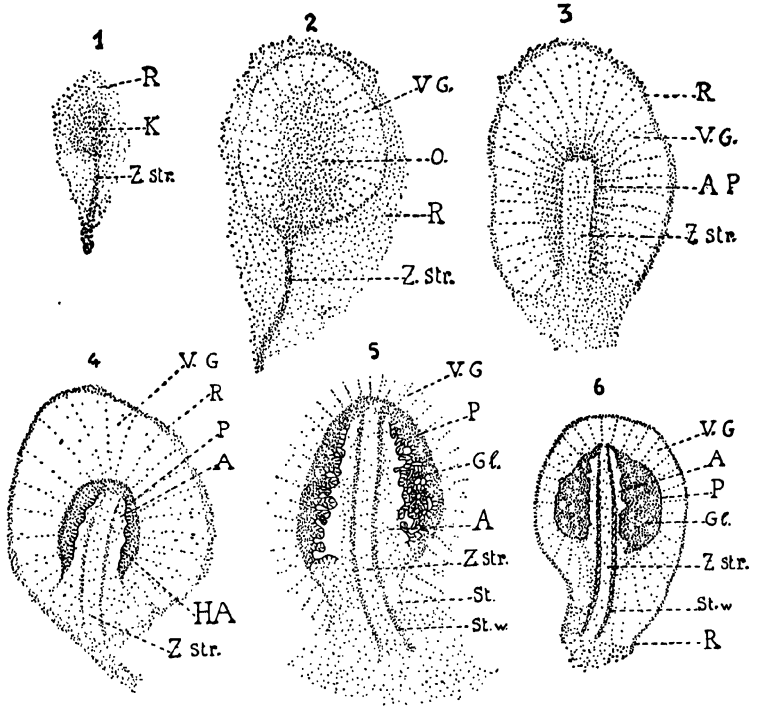


FIG. 332.—*Mutinus caninus.* Development of fructification. (1, 2 × 70; 3 × 44; 4, 5 × 24; 6 × 6; *after Burt*, 1896.)

stipe walls of the receptacle. The members of its hyphae swell gradually so strongly that the chamber walls in the lower part of the receptacle stipe lie in folds. This receptacle corresponds to the receptacle stipe of *Colus, Anthurus* and *Aseroe* in the Clathraceae.

A longitudinal section through an immature fructification is given in Fig. 332, 6. The gleba *Gl.* has already darkened, and is separated from the volva gel by a narrow layer, the compressed zone *P*, and from the stipe wall by the vestiges of the intermediate tissue *A*. In the South American *Mutinus Muelleri*, these vestiges become large spherical cells; in *M.*

bambusinus of the tropics, this change occurs only in the proximal portion of the stipe and is entirely absent in *M. caninus* of the north temperate zone.

The habit of a mature fructification is shown in Fig. 333. The stipe of the receptacle is white or reddish, the sporiferous part is dirty purple-red. The pileus is lacking and the gleba lies directly on the sides of the receptacle.

In the other genera of the Phallaceae, the fructifications are formed according to the plan of *Mutinus*, but the intermediate tissue *A* undergoes a higher differentiation.

A first step in this direction, we find in *Phallus tenuis* of southern Asia (E. Fischer, 1887). In it, the top of the tramal plates which press inward toward the layer *A* are not, as in *Mutinus* (and in the Hysterangiaceae), covered with a hymenial palisade. Their hyphae develop (as *mutatis mutandis* in *Hysterangium* of the Hysterangiaceae) into the intermediate tissue *A* and connect laterally with the outgrowing hyphae of the neighboring tramal plates. Thereby a continuous layer *H*, divided by elevations and depressions (Fig. 335), shuts off the gleba chamber on the inside. At its apex it connects with the top of the stipe wall (receptacle); further down it is separated from the stipe wall by the remains of the layer *A*. The gleba does not lie directly on the stipe, as in *Mutinus*, but on the new campanulate tissue plate, which subsequently becomes the pseudo-parenchymatous pileus of the young fructification. When, at maturity, the receptacle elongates by straightening the folded chamber walls, the pileus with the gleba is raised out of the volva gel and the gleba drops off. The representation of such

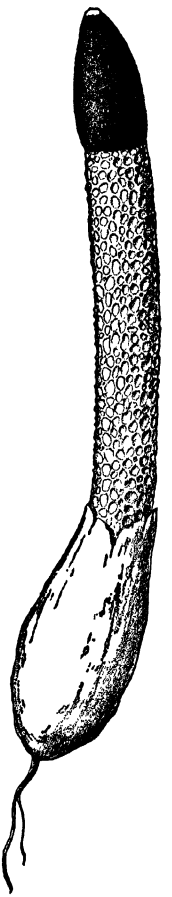


FIG. 333.—*Mutinus caninus*. Mature fructification, showing gleba. (Natural size; *after Fischer*, 1900.)

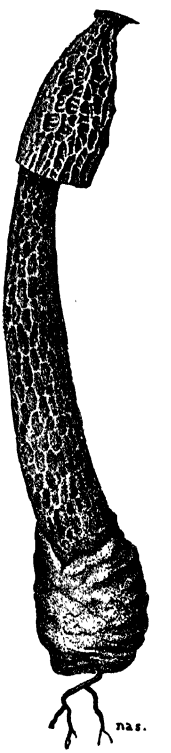


FIG. 334.—*Phallus tenuis*. Unfolded fructification after disappearance of gleba. (Natural size; *after Fischer*, 1887.)

a fructification whose gleba has already flowed away is given in Fig. 334; in nature, it is isabelline.

In *Phallus impudicus* (E. Fischer, 1891, 1893; Bambeke, 1910), the development proceeds in such a manner that the layer *A* undergoes a stronger development and in the stage corresponding to that shown in *Mutinus* (Fig. 332, 4) and *P. tenuis* it is differentiated into three layers

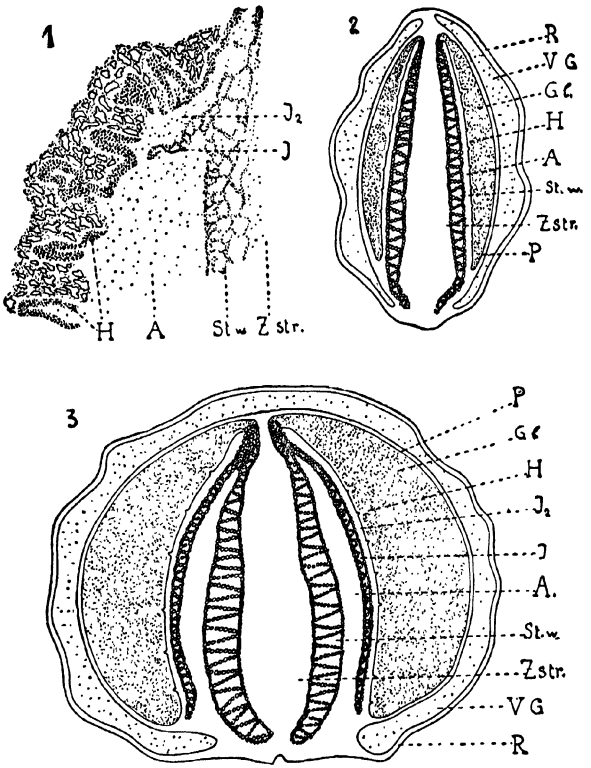


FIG. 335.—*Echinophallus Lauterbachii.* 1. Median section of upper portion of fructification. *Phallus tenuis.* 2. Median section of mature egg. *Dictyophora indusiata.* 3. Median section of mature egg. (2, 3 × 2; *after E. Fischer*, 1887, 1900.)

(Fig. 336, 1). The outermost zone *H*, directly bordering on the tramal pads, assumes a somewhat different character and is more refractive. The middle, thick zone *I* is campanulate and parallel to *H* but, instead of reaching the columella, passes over laterally into knotted cover *St.w.* The inner zone *A* has a structure corresponding to that of the original intermediate tissue with hyphae more or less definitely radiating from the stipe axis toward the periphery. From the layer *H* and from the

outermost part of *I*, the pileus of the receptacle arises, as in *P. tenuis*, but with less cooperation of the hyphae radiating from the tramal plates. The layer *A* and the greater part of *I* develop no further; they remain as simple hyphal tissue and are torn and destroyed by the unfolding of the receptacle. In the mature egg, differentiation is similar to that of *P. tenuis* but the vestiges of the tissue *A* (*A* and the inner part of *I*) occupy much more space than in the latter. The part which interests us here, corresponding to the top in Fig. 336, 1, is given in Fig. 336, 2 for a somewhat older stage. The small projection *V* suggests the spot where in Fig. 336, 1 the inner layer *I* was attached to the stipe wall.

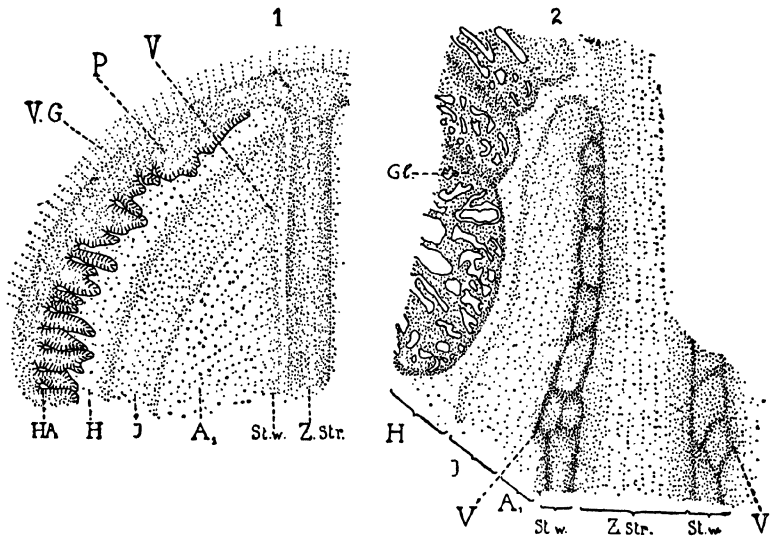


FIG. 336.—*Phallus impudicus*. Median section of top of young fructification. (× 18; *after E. Fischer*, 1891, 1893.)

This species is popularly called stink horn. Its eggs are eaten at times in Europe. Earlier both these and the ripe fructifications were used as drugs in the preparation of salves and powders for rheumatism and pestilence.

In the Polynesian *Echinophallus Lauterbachii* (Fig. 335, 1), which is known only in the young stages, the zone *I* increases markedly at the expense of zone *H* (E. Fischer, 1900) which is very narrow and much curved outwards. In contrast to *Phallus* and the other Phallaceae here discussed, it forms no continuous layer but is discontinuous like a lattice. In longitudinal section (Fig. 335, 1) it shows only as short pieces, separated from one another and much enfolded in the gleba.

At approximately two-thirds of its height, there arises a campanulate appendage *I*, 2 to 3 mm. broad, consisting of a simple layer of closed cham-

bers filled with gel like those of the stipe wall. Similarly, there arises a small projection *V* which in *Echinophallus* attains a greater development (Fig. 336, 1, 2). The space between it and the pileus *H* is occupied by an opaque gel *I* which in some spots is directly connected with the gel of

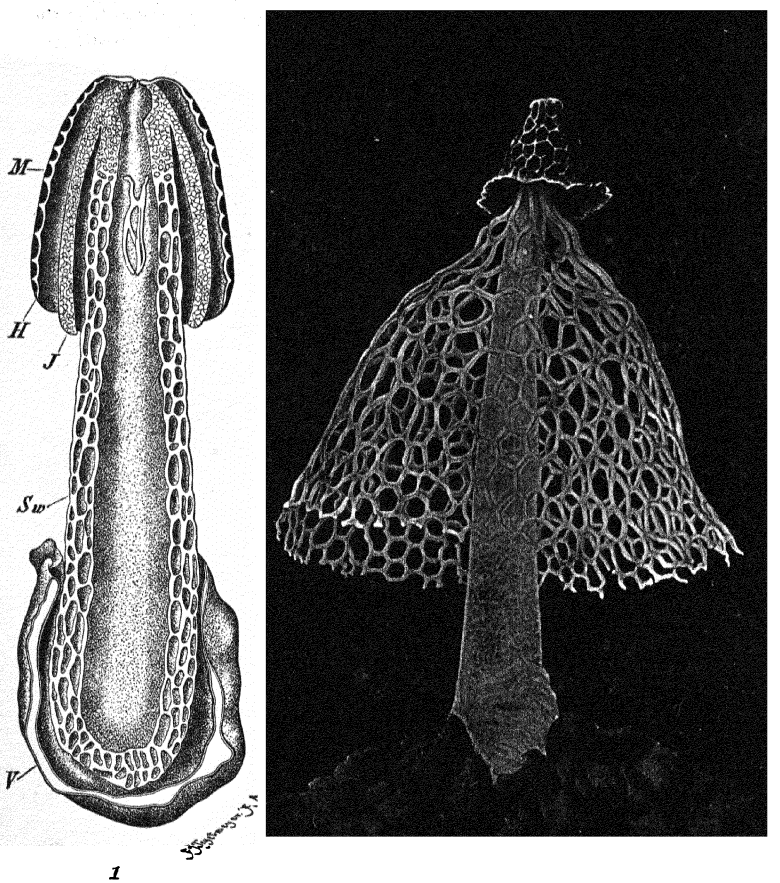


FIG. 337.—*Dictyophora indusiata.* 1. Section of fructification in which the stipe of the receptacle has elongated and the gleba has mostly disappeared while the indusium is folded and hidden under the pileus. 2. Fructification, showing unfolded indusium. (1, natural size; 2 × ⅔; *after E. Fischer*, 1887, and *Möller*, 1895.)

the stipe chamber. Below the zone *I*, in the space between the stipe wall *St.W.* and the pileus, *i.e.*, the gleba, lies the bluish-gray, comparatively loose tissue *A*. These tissue differentiations have arisen in the same manner as their homologues in *P. impudicus;* there they have vanished

in the course of development and consequently in the stage of Fig. 336, 1 are recognizable as such only in the apical end of the egg.

This tissue *I* reaches its greatest development in *Dictyophora;* here it develops to a beautiful structure (E. Fischer, 1887, 1890, 1891, 1900, 1910; Moeller, 1895; Burt, 1897; Atkinson, 1911). It is chambered, like the receptacle, and follows the inner side of the pileus from the top to the base of the egg (Fig. 335, 2). When the stipe elongates at the unfolding of the fructification, the layer *I*, together with the pileus and the gleba lying on it, is raised. Then the folded chamber walls elongate in this layer, as did the receptacle stipe (Fig. 337, 2), and the layer *I* expands like a crinoline toward the bottom and unfolds to a latticed indusium. This indusium is only an appendage of the receptacle stipe and, in contrast to the pileus, is not directly connected with the gleba. It is formed when the gleba is just beginning to form and its ends are still far removed from the stipe. Its significance is not yet clear.

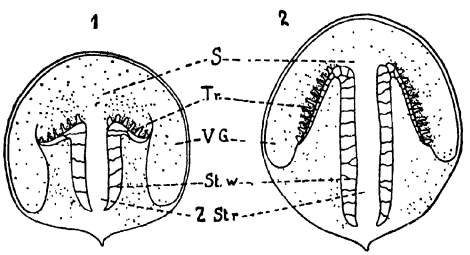


FIG. 338.—Section of hypothetical transitional form between *Aseroë* and the Phallaceae. 2. Diagram of young fructification of *Phallus*. Letters as in Fig. 332. (*After E. Fischer*, 1910.)

A majority of the Clathraceae and Phallaceae are entomochorous and by their strong odors attract attention from a distance. The fructifications generally unfold at night and at dawn, the gleba has mostly dropped off.

As Lohwag (1924) has demonstrated, in this grouping the Phallaceae would be regarded as derivatives of the Clathraceae. In both families the organization is fundamentally the same, only in the former the tramal plates grow centripetally, in the latter centrifugally. If one imagines that the development which leads from *Protubera, Clathrella, Anthurus* through *Aseroe arachnoidea* to *Aseroe rubra,* continues, and that the widening of the central strand *S* (Fig. 330, 7), appearing above the stipe orifice, is more strongly developed and arched over slightly with the edge in the shape of a bell, and that the splits between the branches of the columella and thereby the plates of the intermediate tissue and the receptacle branches (which in *Aseroe rubra* have been already alienated from their original function) progressively degenerate and finally disappear, one arrives at a form like that represented schematically in Fig. 338, 1. Its longitudinal section is like that of *Aseroe rubra,* but the receptacle

branches are rudimentary and the intermediate tissue is limited to the basal half of the fructification. Also the letters are changed to correspond to those in the scheme for the Phallaceae.

From this form, the transition to a simple species of *Phallus*, *e.g.*, *P. tenuis*, is easy. It must be remembered, however, that the intermediate form represented in Fig. 338, 1 is only a theoretical construction and has not yet been found, and that it is still uncertain whether we may regard the *Phallus* as primitive or whether, perhaps, some of its species, *e.g.*, *P. impudicus*, should not be regarded as degenerate species of *Dictyophora* with reduced indusium. Similarly, it is still uncertain whether *Mutinus* may be considered a degenerate form, as by this conception, it must seem even more primitive in several respects. It is further obvious that even if these intermediate forms were found, it would not yet be proved that the development proceeded in the manner suggested. This derivation of the Phallaceae from the Clathraceae through *Aseroe* and *Phallus* seems much more probable than the other possibility. It is more plausible than the direct derivation of the Phallaceae from the *Endoptychum*, for it would be difficult to understand why, as an indication of convergence, the Clathraceae and Phallaceae have attained an equal stage in differentiation of their tissues, when there were so many other possibilities.

The transition from the Clathraceae to the Phallaceae is marked by the following three points: the plates of intermediate tissue, which in the Clathraceae cause a separation of the volva gel into plates, have entirely disappeared after *Aseroe* so that in the Phallaceae, the volva gel forms a continuous cap. Similarly, the development of the central strand is backward and no longer divides. And, thirdly, the development of the gleba, which in *Aseroe rubra* is removed from the central strand, in the Phallaceae is shifted outwards and connected with this strand at its upper end only.

A schematic presentation of these mutual relationships is given on page 519. With increasing knowledge, the above systematic classification of the Gasteromycetes, like that of the Polyporales and Agaricales, will undoubtedly be entirely rearranged.

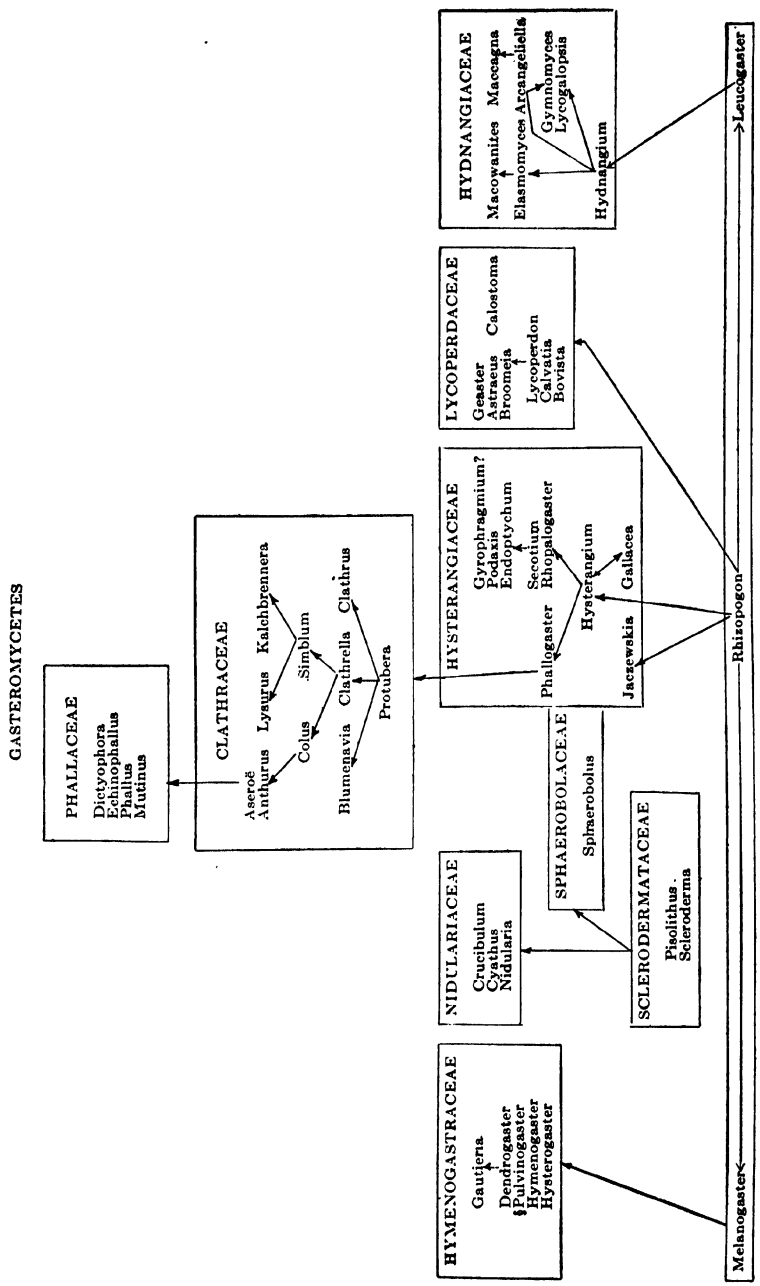

GASTEROMYCETES
PHALLACEAE
Dictyophora
Echinophallus
Phallus
Mutinus
CLATHRACEAE
Aseroë
Anthurus
Lysurus
Kalchbrennera
Colus
Simblum
Blumenavia
Clathrella
Clathrus
Protubera
HYSTERANGIACEAE
Gyrophragmium?
Podaxis
Endoptychum
Secotium
Phallogaster
Rhopalogaster
Hysterangium
Jacqewskia
Gallacea
LYCOPERDACEAE
Geaster
Astraeus
Broomeia
Calostoma
Lycoperdon
Calvatia
Bovista
HYDNANGIACEAE
Macowanites
Maccagnia
Elasmomyces
Arcangeliella
Gymnomyces
Lycogalopsis
Hydnangium
NIDULARIACEAE
Crucibulum
Cyathus
Nidularia
SPHAEROBOLACEAE
Sphaerobolus
SCLERODERMATACEAE
Pisolithus
Scleroderma
HYMENOGASTRACEAE
Gautieria
Dendrogaster
Fulvinogaster
Hymenogaster
Hysterogaster
Rhizopogon
Melanogaster
Leucogaster

DIAGRAM XXX.

CHAPTER XXIX

TREMELLALES

In the Tremellales, we return again to the threshold of the Basidiomycetes. They represent the chiastobasidial counterpart of the Auriculariaceae and have rounded, pyriform basidia, longitudinally divided into four cells. They begin as the Polyporales with forms without well-developed fructifications and end with forms having gymnocarpous or even angiocarpous fructifications. The gymnocarpous species are placed in the Tremellaceae, the angiocarpous ones in the Hyaloriaceae, while two species of doubtful position are placed in the sirobasidiaceae. Their most marked morphological relationships are shown in the scheme below.

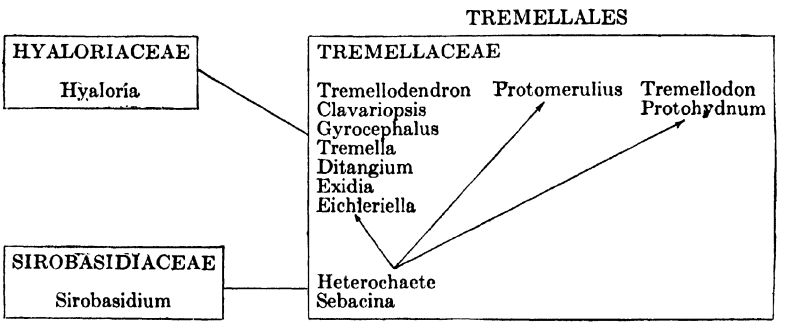


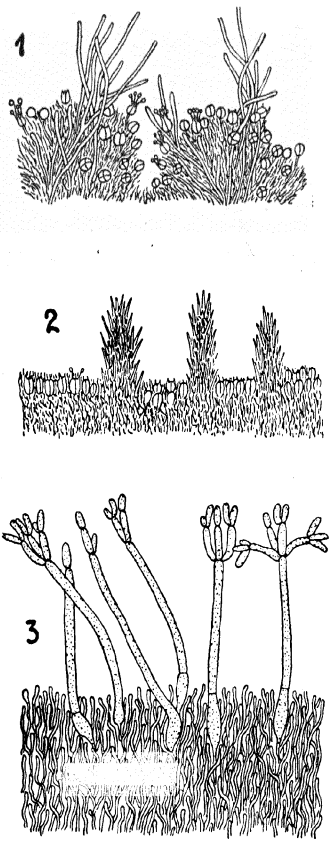
DIAGRAM XXXI.

Tremellaceae.—This family forms a series parallel to the Polyporales, developing from arachnoid coverings to compact, bilateral, gymnocarpous fructifications. According to the structure of these fructifications, they may be divided into four subfamilies: the Sebacineae, the Tremelleae, the Protomerulieae and the Tremellodonteae.

The Sebacineae correspond to *Corticium* of the Corticiaceae. In the primitive forms with cruciate basidia, there is no well-defined hymenium, the basidia appearing irregularly scattered on the mycelial felt. *Sebacina papillata* (*Stypella papillata*) and *S. minor* (*Stypella minor*) (Möller, 1895) on mouldy wood in Brazil, form small, gelatinous coverings with papillose elevations which consist of peculiar, long, tubular, aseptate cells (Fig. 339, 1). At the ends of hyphae, the cruciate basidia

develop at variable heights above the substrate. Occasionally the second septum fails to develop in them.

In the higher forms, the hyphal tissue is waxy, membranous or coriaceous and the basidia form smooth hymenia. *Sebacina uvida* (*Exidiopsis effusa*) is also poorly developed. The basidiospores germinate with falcate conidia of the *Auricularia* type (Brefeld, 1888). Before basidia develop, thick branches of the subhymenial hyphae form special conidiophores which project above the hymenium and cut off little heads of



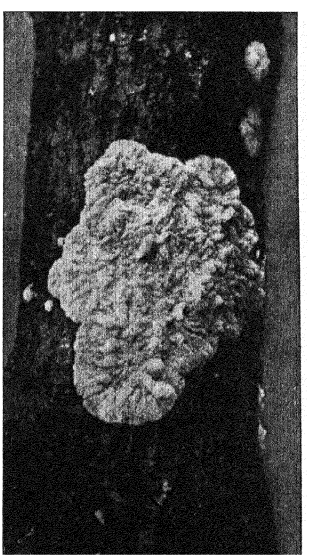


FIG. 339. FIG. 340.

FIG. 339.—1. *Sebacina minor.* Showing irregularly arranged basidia in hyphal tissue. 2. *Heterochaete Sanctae-Catharinae.* Section of fructification, showing portion of hymenium. 3. *Sebacina incrustans.* Young hymenium, showing conidiophores. (1 × 180; 2 × 100; 3 × 270; *after Brefeld,* 1888, *and Möller,* 1895.)

FIG. 340.—*Sebacina ciliata* (*Exidiopsis ciliata*). Habit. (Natural size; *after Möller,* 1895.)

long, oval, conidia (Fig. 339, 3). In *Sebacina* (*Bourdotia*) *gloeocystidiata* (Kuehner, 1926), caryogamy occurs in the young basidium followed by meiosis and the formation of the usual septa. The basidiospores are uninucleate. *Heterochaete Sanctae-Catharinae* (Möller, 1895), in Brazil, appears on tree trunks as resupinate, very thin, gelatinous

membranes, with irregular borders, covered between the setae by an even hymenium (Fig. 339, 2).

The Tremelleae bear the same relation to the Sebacineae as *Stereum* to *Corticium*, or *Auricularia* to *Platygloea*, only their fructifications are even

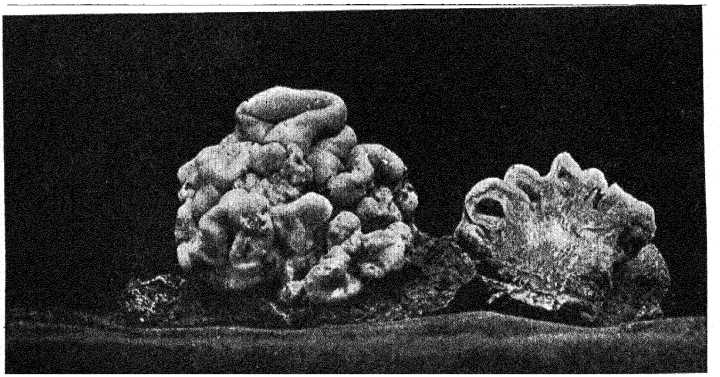


FIG. 341.—*Tremella compacta*. Habit and cross section. (Natural size; *after Möller*, 1895.)

more gelatinuous than those of *Auricularia*. These gelatinous masses are hygroscopic, having the ability to swell greatly in wet weather, while in dry weather the imbibed water readily evaporates, producing great

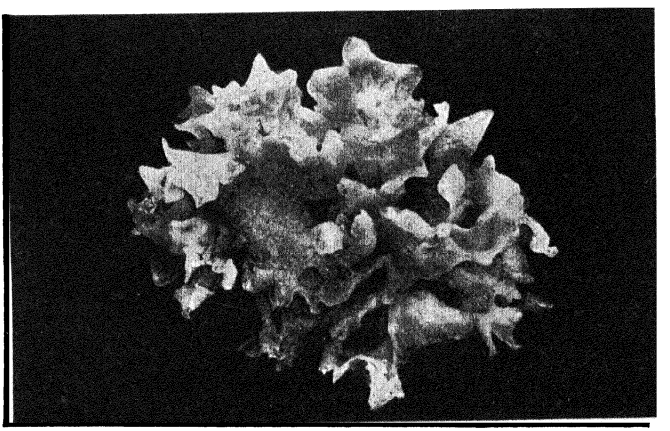


FIG. 342.—*Tremella fuciformis*. Habit. (Natural size; *after Möller*, 1895.)

shrinkage and change of form, as well as practical suspension of life processes. With the return of rainy weather, they renew their growth and spore formation. They are very resistant to temperature changes and endure −20° C. without injury.

The systematic differentiation of these forms is very difficult because marked morphological characters are lacking and because the form of the fructifications, depending upon their environment, may alter beyond recognition. The conidia are, therefore, often used to distinguish the genera.

The simpler genera, as *Eichleriella*, *Exidia* (*Ulocolla*), *Ditangium* (*Craterocolla*) and *Tremella*, are directly connected with *Sebacina* in the structure of the fructifications. *Eichleriella* is more or less coriaceous and bears the same relation to *Sebacina* which *Stereum* and *Cyphella* bear to *Corticium*. *E. spinulosa* has a tuberculate hymenium resembling *Radulum* and forms a transition to *Protohydnum* in the Tremellodonteae. The other genera are gelatinous to cartilaginous, tuberiform to turbinate, generally much lobed and branched, often cerebriform (Figs. 341 and 342), bearing a hymenium on the outer surface, but sterile next the substrate.

The higher genera, *Gyrocephalus*, *Clavariopsis* and *Tremellodendron* develop forms reminiscent of the higher families of the Polyporales. *Gyrocephalus* forms stipitate, infundibuliform fructifications, bearing the hymenium on the inner side. In form they suggest *Craterellus cornucopioides* and the Cantharellaceae. *Clavariopsis* forms cylindric or coralloid fructifications similar to *Clavaria*, while *Tremellodendron* has flattened branches, resembling *Sparassis*, *Pterula* or *Thelephora*.

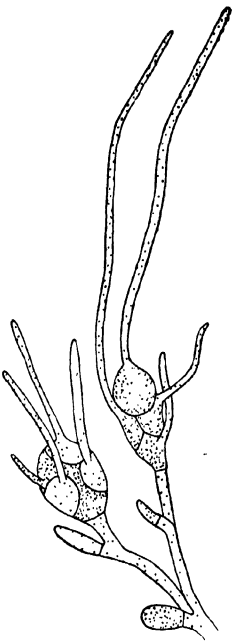


FIG. 343.—*Tremella lutescens*. Basidium with irregular septa, germinating to mycelium. (× 720; *after Coker*, 1920.)

In the basidia, the spindle is transverse at the division of the diploid nucleus. At the end of the first division, the first septum is laid down from the basidial wall. The nuclei divide again, their spindles are transverse and approximately parallel to the first septum, hence perpendicular to the plane of division of the first nucleus. After this division, a new septum is formed perpendicular to the first (Juel, 1898; Neuhoff, 1924; Kuehner, 1926). In the rare cases where the septa are not always transverse, *e.g.*, in *Tremella compacta*, they may be parallel, as in the *Auricularia* type, or in *T. lutescens*, they may be irregular, (Fig. 343), or they may be absent. Sometimes the basidia, instead of forming spores, may develop directly to mycelia. In *Clavariopsis prolifera*, as in *Eocronartium* and *Iola*, new basidia are always formed by lateral growth of the subterminal cells on the same hypha.

The germination of basidiospores has only been reported in the last three genera. A basidiospore of *Exidia repanda* divides into two daughter

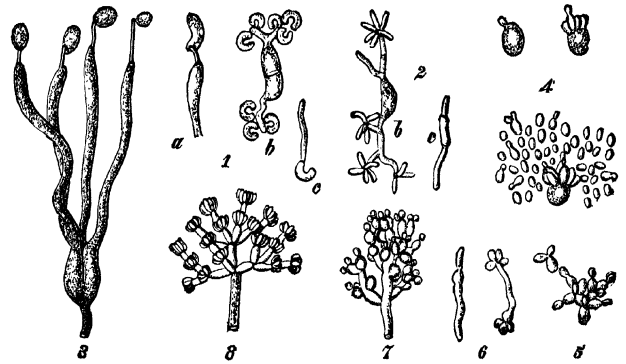


FIG. 344.—*Exidia repanda.* 1. *a*, tip of mature sterigma with reniform basidiospore; *b*, germination of basidiospore with falcate conidia. 2. *Exidia saccharina*, var. *foliacea.* (*Ulocolla foliacea*). *b*, germinating basidiospore; *c*, germinating conidia. *Tremella lutescens.* 3. Mature basidium. 4. Germinating basidiospores, one surrounded by sprout cells. 5. Sprout mycelium. 6. Sprout cells developing hyphae. 7. Conidiophores. *Ditangium Cerasi* (*Orbilia rubella*). 8. Conidiophore. (1*a*, 3 × 450; 1*b*, 5, 6 × 500; 1 *c*, 7 × 420; 2 × 320; 4 × 400; 8 × 300; *after Brefeld,* 1888.)

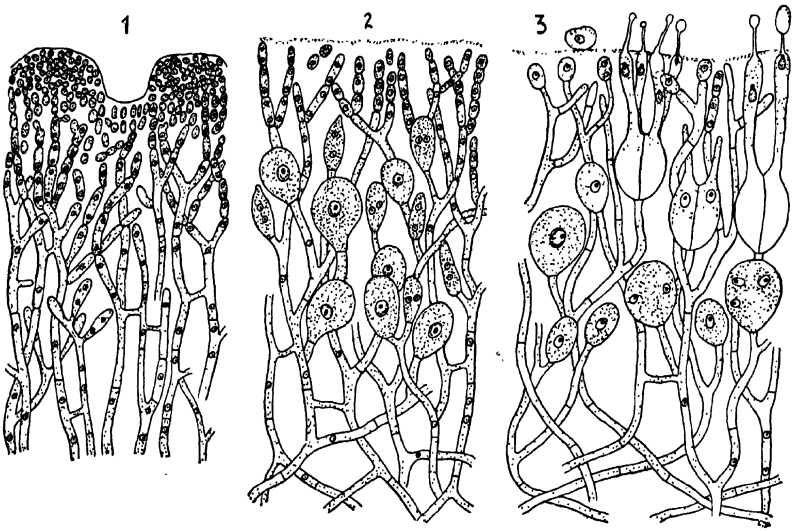


FIG. 345.—*Tremella mesenterica.* Section through periphery of young fructification. 1. Oidial stage. 2. Beginning of basidial formation. 3. Mature basidia. (× 600; *after Dangeard,* 1894.)

cells which in dilute nutrient solutions develop directly to slender septate mycelia without clamps. In *E. saccharina* var. *foliacea,* bacilliform

conidia are produced (Fig. 344, 2). In *Tremella*, the conidia are spherical, and may sprout in nutrient solution (Fig. 345, 3 to 7). In *Tremella lutescens* they are found in Nature on young, still felt-like fructifications where they are cut off in large numbers on branched conidiophores (Brefeld, 1888). In *T. mesenterica* they are replaced by uni- or binucleate oidia which result from the breaking up of the terminal portions of hyphae (Fig. 345, 1 and 2) and multiply by sprouting (Dangeard, 1895). With the appearance of basidia and the increase of gel secretion, conidial formation decreases and their remains are imbedded in the gel. A similar succession was reported

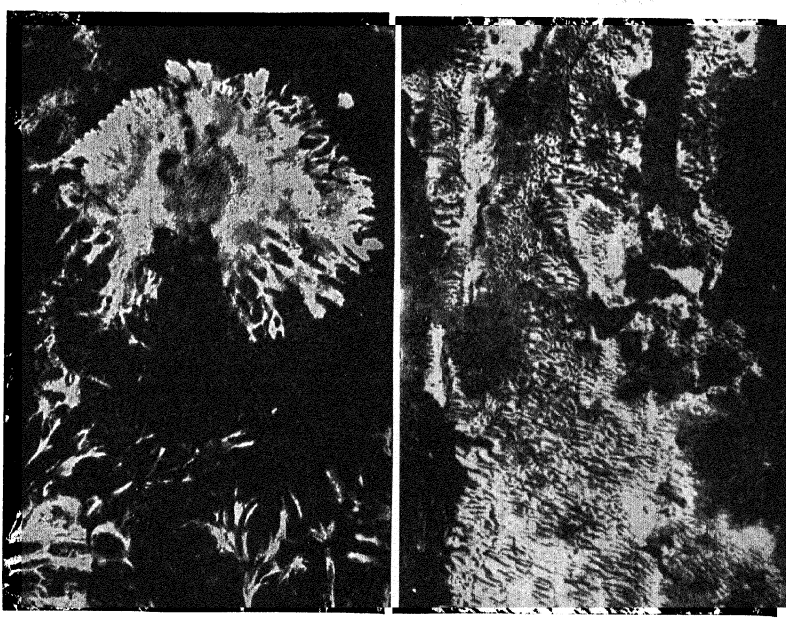


FIG. 346.—*Protomerulius brasiliensis*. Habit. (Natural size; *after Möller*, 1895.)

for *Ditangium*. A young fructification, which appears in the fall, consists of a swollen hyphal felt whose mature top has crateriform openings, covered by stratose, branched conidiophores (Fig. 344, 8). The conidia resemble the basidiospores but are only half as large. During the winter, the hyphal membranes swell, the fructification gelifies and basidia appear. The basidiospores germinate without division either by conidia or germ tubes. As far as known, the secondary spores formed on the mycelium are uninucleate, those on the fructifications binucleate (Neuhoff, 1924); hence the former are haploconidia, the latter diploconidia.

In the Protomerulieae, the convolutions of *Exidia* become folds and reticulations. In *Protomerulius brasiliensis* (Möller, 1895) and *P. Farlowii* from New Hampshire (Burt, 1919, *a*) the reticulations gradually grow upwards, producing a tangle of tubes resembling the hymenium of *Merulius* (Fig. 346). Bracket forms, somewhat resembling *Auricularia*, are sometimes formed under favorable conditions.

Similarly, the Tremellodonteae resemble the resupinate genera of the Radulaceae, *e.g.*, *Tremellodon cartilagineum* (Möller, 1895). In *Proto-*

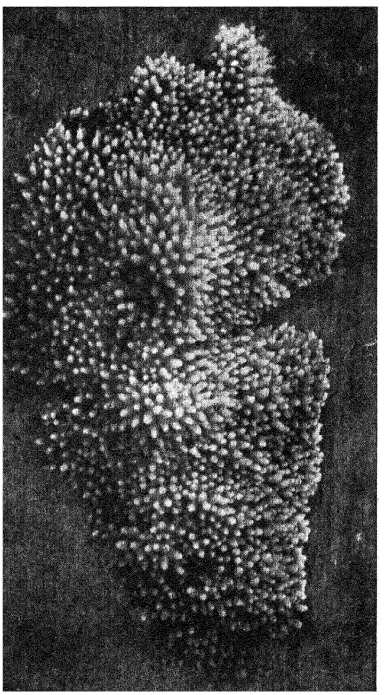


FIG. 347.—*Tremellodon cartilagineum.* Habit. (× ¾; *after Möller*, 1895.)

hydnum lividum, var. *piceicola*, Kuehner (1926) reports the usual nuclear phenomena in the basidium and young basidiospores. In the highest form, *Tremellodon gelatinosum* (*T. crystallinum*), the fructifications are often laterally stipitate with teeth resembling those of the higher Radulaceae (Fig. 348).

Hyaloriaceae.—This family is the angiocarpous homologue of the Phleogenaceae and Gasteromycetes. The basidia arise irregularly within the fructification, and are not united into hymenia. The only well-known

species, *Hyaloria Pilacre* (Möller, 1895), forms shining, almost transparent stipes which taper upwards and bear at the tip a small head (Fig. 349). This consists of a tangled felt of slender hyphae imbedded in a gel. The hyphae radiate toward the outer wall, within which they form on branches, a compact layer of cruciate basidia. The structure of the fructification is similar to that in *Phleogena*, except the hyphal ends remain smooth and do not coil, allowing the spores to be liberated between them.

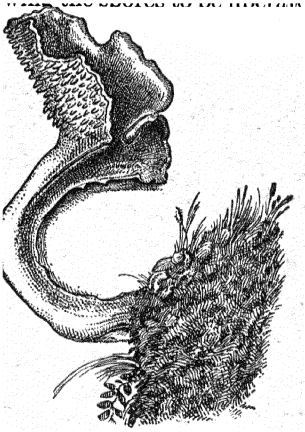


FIG. 348.—*Tremellodon gelatinosum*. Habit. (Natural size; *after Möller*, 1895.)

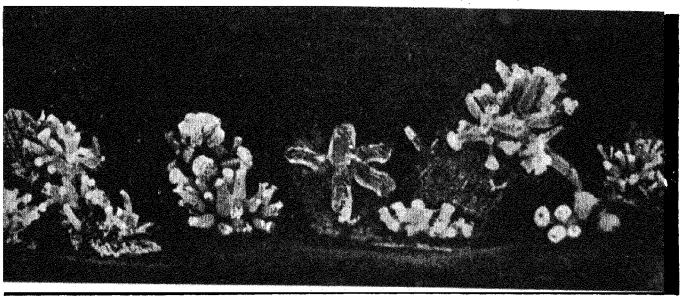


FIG. 349.—*Hyaloria Pilacre*. Habit. (Natural size; *after Möller*, 1895.)

Sirobasidiaceae.—As an appendix, we will discuss two interesting forms whose position is still obscure. *Sirobasidium Brefeldianum*, on rotting wood in Brazil, forms shining, later white, gelatinous fructifications up to 3 mm. in diameter. They consist of numerous, loosely tangled hyphae radiating from a single point and imbedded in a transparent gel (Fig. 350, 1). Clamps are abundant at the septa. The terminal cell of the hyphae swell to elongate ovoids and divide by usually oblique

septa into two daughter cells, each of which cuts off a basidiospore without a sterigma. The next cell below then swells and repeats the process basipetally. The basidiospores germinate with germ tubes or sprout conidia. *S. albidum*, on dead twigs in Ecuador, has true four-celled cruciate basidia.

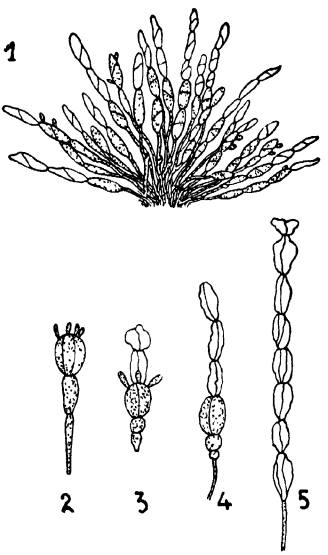


FIG. 350.—*Sirobasidium Brefeldianum*. Habit, enlarged, showing basidia. (× 145; *after Möller*, 1895.) *Sirobasidium albidum*. 2 to 5. Development of basidia. (× 250; *after Lagerheim and Patouillard*, 1892.)

Whether these two species are related to each other and are rightly placed in the same genus, can only be decided by their cytological relations. Möller (1895) considered them as transition forms between the Phragmobasidiomycetes and the Autobasidiomycetes, which latter had developed from the former by a change in orientation of the basidial walls.

CHAPTER XXX

CANTHARELLALES

The Cantharellales ascend, as do the Polyporales, from resupinate types to gymnocarpous forms. Anatomically, even the highest forms retain primitive characters, the uniform structure and slight differentiation of hyphal tissue, hymenophore and hymenium. The basidia correspond to the stichobasidial type, simple in form and variable in spore number. The diploid nucleus (as in asci) generally proceeds through three divisions, hence the young basidium is octonucleate and in this condition appears entirely similar to a Hypocreaceous or a Discomycetous ascus (Fig. 353, 3). Similarly, in some species, usually eight basidiospores are formed; in others, in spite of the octonucleate basidia, the spore number is reduced and finally fixed at a two-spored type, although the stichobasidial method of division is retained (Fig. 353, 10). These two-spored basidia suggest conditions we will find in the Dacryomycetales, since their sterigmata often swell at the base, forming a cone. Perhaps both orders have developed from simple resupinate crusts with normally eight-spored basidia. At present no imperfect forms are known, but two parasitic genera have been reported to form sprout mycelia.

As already briefly indicated on page 427, the Cantharellales is only a provisional order. This transitional state is explained by the lack of cytological information. Until this has been obtained, it seems better to leave the species in the chiastobasidial orders, which are much larger and have realized more varied possibilities of development than the stichobasidial type. Therefore we will place in the Cantharellales only those forms in which stichobasidia have been demonstrated, and make no nomenclatorial changes to carry out this classification. The value of this separation of the stichobasidial types from the chiastobasidial types is extremely doubtful (Juel, 1916).

These forms may be placed in three families: the Exobasidiaceae, resupinate forms, often modified by their parasitism, usually lacking a compact hymenium, so that their basidia emerge singly or in groups from the stomata of the host; the Clavulinaceae with fructifications similar to those of the Clavariaceae discussed in the Polyporales; and the Cantharellaceae, whose fructifications are differentiated into pileus and stipe. Their possible phylogenetic relations are shown in the following diagram:

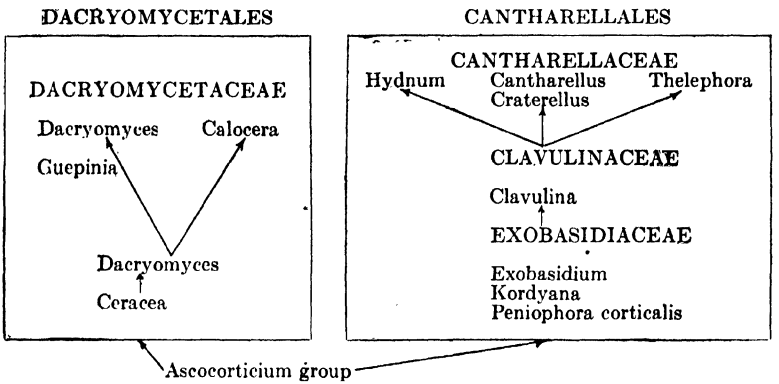


DIAGRAM XXXII.

Exobasidiaceae.—This family, usually included in the Corticiaceae by systematists (*e.g.*, Burt, 1915), contains primitive, resupinate species. The only saprophytic species, *Peniophora corticalis* (*P. quercina*, *Kneiffia corticalis*), forms resupinate crusts on twigs. The hyphal cells are originally binucleate but later, by nuclear division without septation, they become multinucleate (Maire, 1902). Clamp connections are abundant. The smooth hymenium consists of four-spored basidia and cystidia which are sunk deep, so that only the tips project beyond the basidia. All the other species of this genus which have been investigated belong to the chiastobasidial type. The germination of the basidiospores is unknown.

Kordyana is parasitic on leaves of tropical species of Commelinaceae, causing brown spots, surrounded by a light green zone. The hemispherical hymenia, white or yellowish, are erumpent from a hyphal tissue in the substomatal air passage on the underside of the spots (Fig. 351). They consist of basidia and sterile hyphae (paraphyses) exceptionally of basidia only. The basidia are rather variable in form. At maturity they generally contain four nuclei; usually producing two spores. In damp nights, there may be formed successively, small fascicles of as many as six spores in which mature and immature spores are intermingled. They germinate either by germ tubes or by sprout mycelia (Gäumann, 1922).

Exobasidium biologically bears a relationship to *Kordyana*, similar to that of *Albugo* and *Peronospora* to the Pythieae in the Oomycetes. The hyphae of *Kordyana* penetrate the infected tissue in all directions and kill it; those of *Exobasidium* have adapted themselves to the host and stimulate it to form galls and witches' brooms, rather than kill it. In this respect, *Exobasidium* resembles *Taphrina* in the Ascomycetes.

Exobasidium Vaccinii, parasitic on many Ericaceae, especially on *Vaccinium Vitis-Idaea* (Fig. 352), has been studied in great detail (Woronin, 1867; Brefeld, 1889; Maire, 1902; Burt, 1915; Eftimiu and

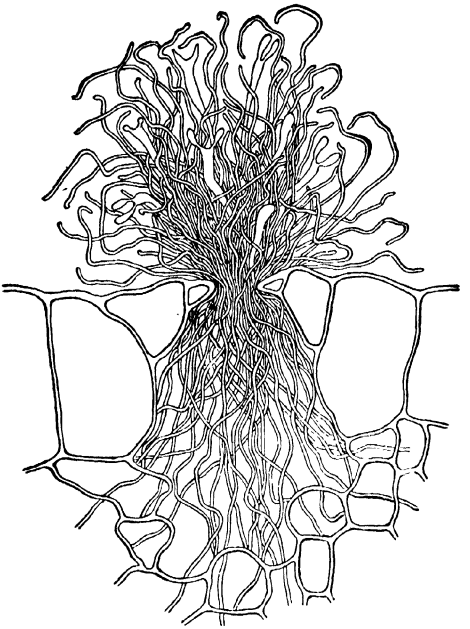


FIG. 351.—*Kordyana Polliae.* Section of hymenium on underside of leaf. (× 450; *Gaumann*, 1922.)

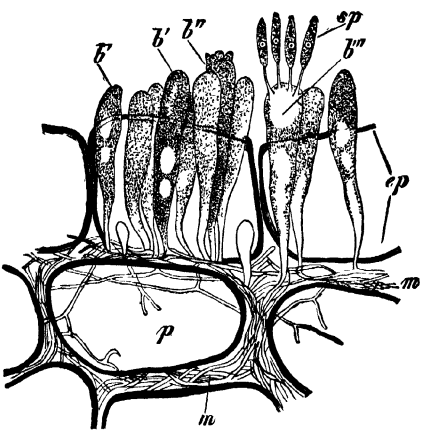


FIG. 352.—*Exobasidium vaccinii.* Section of periphery of stem of *Vaccinium Vitis-idaea*, showing hymenium; *ep*, epidermis; *p*, bark parenchyma; *m*, hyphae in intercellular spaces; *b*, erumpent basidia; *b'*, basidium, still without sterigmata; *b''*, basidium after formation of sterigmata; *b'''*, basidium with mature basidiospores. (× 620; *after Woronin*, 1867.)

Kharbush, 1927). The hyphae occupy intercellular spaces. The cells of the host are stimulated to hypertrophy and hyperplasia, forming swellings on the leaves or thickening and lengthening of the whole shoot. The chlorophyll is destroyed and replaced by red pigment. The basidia (in contrast to *Kordyana*) penetrate between the epidermal cells and form a thin, white hymenium on the under side of the leaf. They arise singly on hyphal branches, bearing two to six spores. At germination, the spores form one to three septa, each of the cells putting forth a slender germ tube, which, on reaching air, cuts off several narrow, filiform sprout cells, pointed at each end. Sometimes the basidiospores proceed directly to the formation of sprout cells which continue budding without falling off at the tip, thus forming small fascicles. *E. discoideum* on *Azalea* and *E. Rhododendri* on *Rhododendron ferrugineum* frequently have chiastobasidia and should be placed in the Corticiaceae (Eftimiu and Kharbush, 1927).

Clavulinaceae.—This family corresponds in most details to the Clavariaceae as discussed in the Polyporales. At present only four species of *Clavaria* (*sensu latiore*) are known to belong here. The limits of *Clavaria* as given in systematic manuals include both sticho- and chiastobasidial types. As the chiastobasidial forms are more numerous and the type species of the genus occurs among these, the name *Clavaria*, according to the rules of nomenclature, must be limited to the chiastobasidial forms. In this case a new name should be created for the stichobasidial *Clavaria falcata*. Schroeter proposed *Clavulina* for the other stichobasidial species, *C. rugosa*, *C. cinerea* and *C. cristata* (*C. grisea*) on other grounds.

The white or ashy fructifications of these five species grow in damp woods or glades. In *C. falcata*, they are simple and unbranched (subgenus *Holocoryne*); in *C. rugosa*, slightly forked, and in the other three, variously branched, fruticose or dendroid (subg. *Ramaria*). The hyphae bear numerous clamps and in the interior of the fructification are parallel to the axis. At the periphery, they bend perpendicularly and form the hymenium by their compact ends. The hymenium consists of basidia of very unequal age; in old collapsed specimens, one may find very young basidia, which have not yet formed sterigmata.

At maturity, the basidia contain 8 nuclei as a result of a triple division of the diploid nucleus. The number of sterigmata is very variable: in *Clavaria falcata* six to eight, mostly seven, in *Clavulina rugosa*, in time, for they are not formed simultaneously, mostly four, seldom two and in *C. cinerea* (Fig. 353, 6 to 10) and *C. cristata* always two (Maire, 1902; Juel, 1916). As each spore contains only one nucleus, a variable number of nuclei degenerate in the basidium. The third division is sometimes lacking in *C. cinerea* (Bauch, 1927). The germination of basidiospores is unknown. *C. cristata*, *C. cinerea* and *C. rugosa* are edible.

Cantharellaceae.—This family contains the stichobasidial segregates from the Thelephoraceae, Hydnaceae and Agaricaceae of the earlier writers, and is characterized by a differentiation into stipe and pileus. In the young buttons, the hyphae radiate in the upper part and are much branched. As in *Gyrocephalus* of the Tremellales, an infundibuliform structure develops by strong epinastic growth. In *Craterellus*

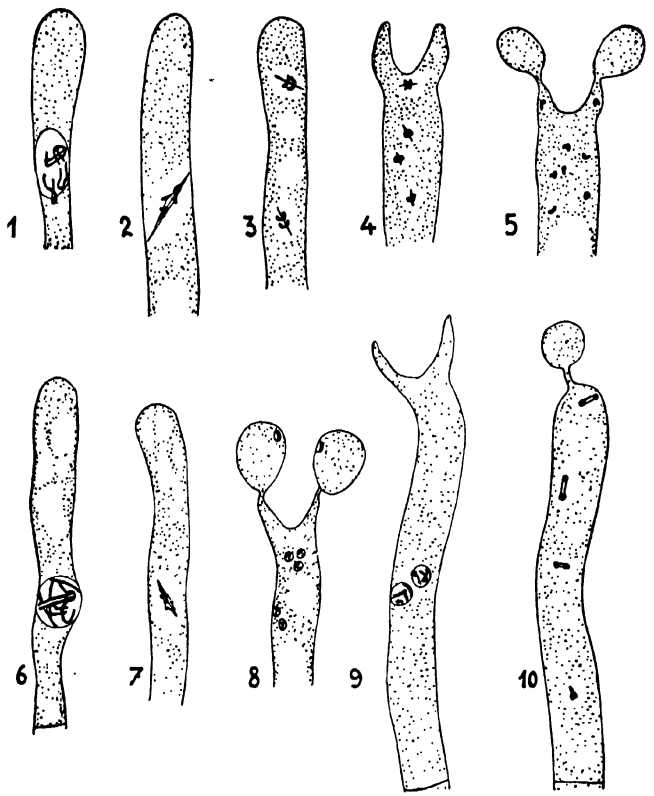


FIG. 353.—Development of basidia of *Craterellus cornucopioides*. 1 to 5. Of *Clavulina cinerea*. 6 to 10. (1 to 5, 10 × 1,200; 6 to 9 × 1,400; *after Juel*, 1916.)

the hymenophore is smooth or slightly wrinkled, in *Cantharellus* it consists of parallel folds similar to the lamellae of the Agaricales, but less well developed. These differences are only quantitative and many intergrading forms are seen.

Cytological investigation extends to only eight species: *Craterellus cornucopioides, C. lutescens, Cantharellus cibarius, C. cinereus, C. tubaeformis, Thelephora palmata, T. anthocephala* and *Hydnum repandum*

(Maire, 1902; Juel, 1916). The structure of the hymenia and basidia agree with that of the stichobasidial Clavariaceae. As in the latter, the diploid nucleus usually, but not always, divides thrice into eight nuclei; the number of sterigmata is variable, *e.g.*, *Cantharellus cibarius* five to seven, mostly six (Fig. 271), *C. cinereus* and *C. tubaeformis* two to five, mostly four, *Craterellus lutescens* three to five, mostly five, and *C. cornucopioides* two to four, mostly two (Fig. 353, 1 to 5). The fate of the remaining nuclei has not been carefully followed. The basidiospores are smooth, hyaline or slightly yellowish.

The fructifications of *Thelephora* correspond to those of the stipitate species of *Stereum* or *Lachnocladium*, being leathery or woody, and more or less infundibuliform or branched. Their hymenium is smooth and confined to the lower surface of the pileus. The basidiospores are echinulate and colored, as in *Hypochnus* of the Corticiaceae.

The fructifications of *Hydnum repandum* bear long teeth on the under side of the pileus, as in the higher Radulaceae. Since this species is the nomenclatorial type of *Hydnum*, the traditional family, Hydnaceae, is considered under the Radulaceae (p. 442).

CHAPTER XXXI

DACRYOMYCETALES

This order is characterized by narrow basidia, apically forked and bearing two basidiospores on long, gradually tapering sterigmata. They ascend from simple forms in which the hymenia are resupinate to those

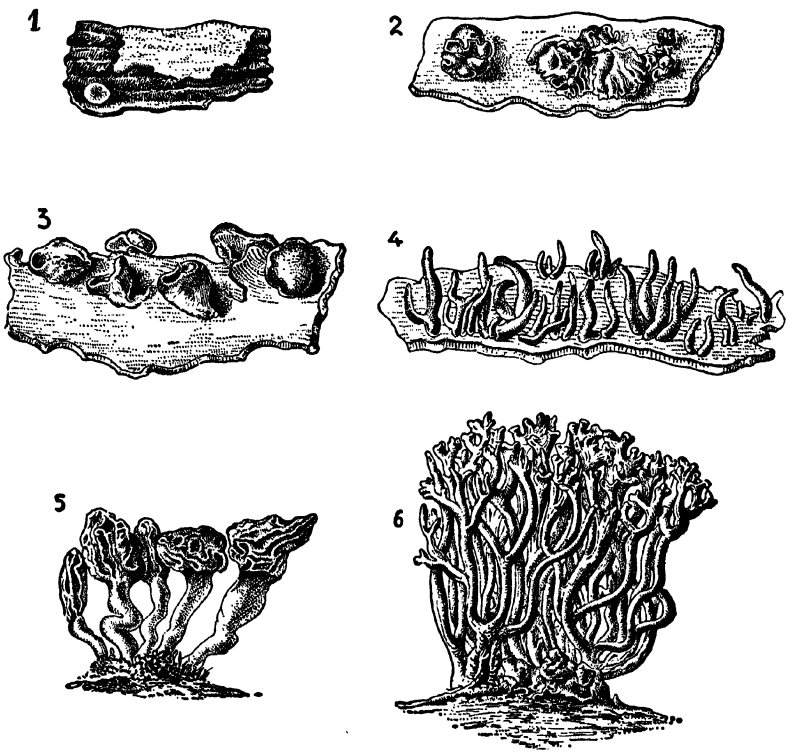


FIG. 354.—Types of fructifications. 1. *Ceracea Lagerheimii.* 2. *Dacryomyces deliquescens.* 3. *Guepinia femsjoeniana.* 4. *Calocera cornea.* 5. *Dacryomitra glossoides.* 6. *Calocera viscosa.* (All approximately natural size; *after Brefeld and Patouillard.*)

with stipitate fructifications and, in this respect, form a series parallel to the Cantharellales. Their probable relationships are shown in the diagram on page 530 in connection with the Cantharellales. Only a single small family is known.

Dacryomycetaceae.—*Ceracea* and *Dacryomyces* occupy the lowest stage. *C. Lagerheimii* is resupinate on rotting wood in Ecuador and forms thin, flat, waxy crusts with loose hymenia (Fig. 354, 1). In *Dacryomyces* these crusts are thicker, pulvinate, gelatinous when moist, drying cartilaginous, smooth at first, becoming cerebriform in age. They are usually yellow and indistinguishable externally from *Tremella* (Fig. 354, 2). The best-known species, *D. deliquescens*, frequently found in winter on dead wood, has both an oidial (Figs. 355, 1; 357, 4) and a basidial stage of development. Its cushion is tomentose in the early years; the usual hyphae have hyaline, binucleate cells. Between these run thicker hyphae, colored orange-red by a lipochrome; they extend far over the

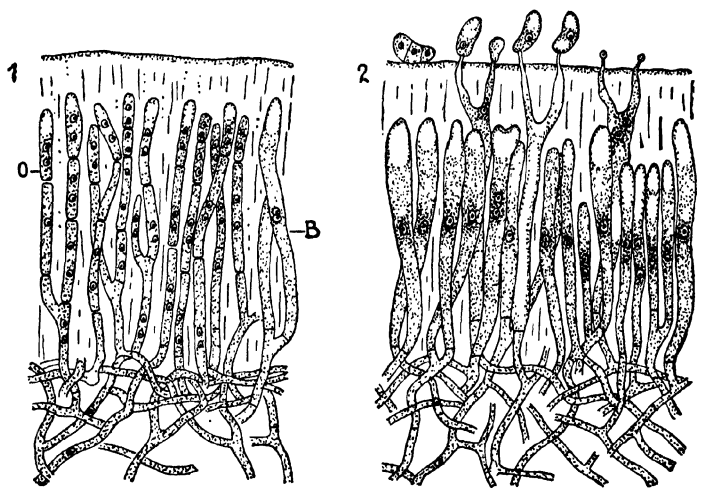


FIG. 355.—*Dacryomyces deliquescens*. 1. Section of fructification with binucleate oidia, *O*, at left; a young basidium, *B*, at the right. 2. Same, with mature basidia. (× 600; *after Dangeard*, 1895.)

stroma and at the periphery break up into an immense number of orange, binucleate oidia which give a yellowish color to the whole stroma. They generally divide before their separation into two daughter cells and, in suitable nutrient solutions, develop to mycelia. In a second or later winter the amber-colored basidia begin to appear on the hyphal cushions; the dark-yellow fructification assumes the consistency of a gel by the gelatinization of the cell walls. As in *Tremella lutescens*, here also a succession of sexual and asexual fructifications are present except that in *Dacryomyces* they extend over several seasons. The basidia arise as thick, binucleate branches of the subhymenial hyphae, and are early arranged in regular hymenia. The dicaryon fuses and meiosis, with longitudinally placed spindles, begins. Meanwhile the basidia have attained full length,

fork at their tip and develop two long sterigmata into each of which a nucleus migrates (Fig. 356, 1 to 3). When the sterigmata have reached the outer surface of the gel, each cuts off a hyaline ovoidal spore, into

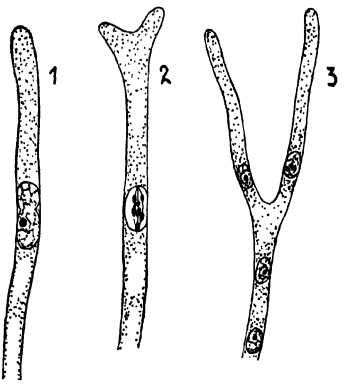


FIG. 356.—*Dacryomyces deliquescens*. Development of basidia. (× 1,330; *after Juel*, 1898.)

which the nucleus migrates. The two nuclei remaining in the basidium degenerate (Gilbert, 1921).

At germination, the basidiospore divides into four daughter cells, each of which cuts off on one or two short germ tubes small fascicles of

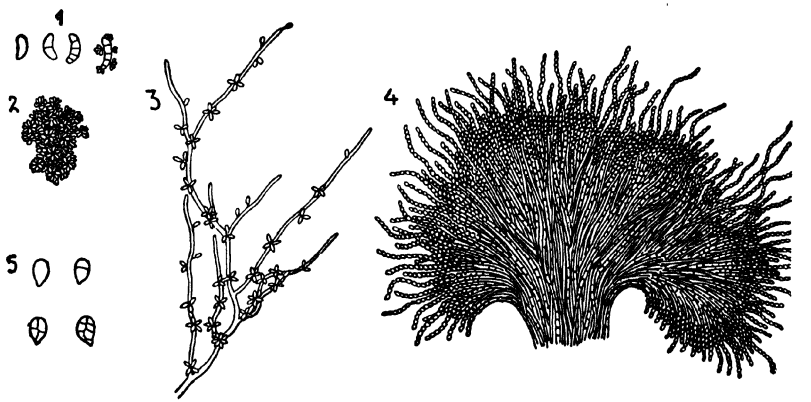


FIG. 357.—*Dacryomyces deliquescens*. 1. Germination of basidiospores in water. 2. Germination in concentrated nutrient solution. 3. Portion of conidial hyphae. 4. Diagrammatic section of an oidial fructification. *Dacryomyces ovisporus*. 5. Germination of basidiospores. (1 to 3 × 240; 4 × 40; 5 × 200; *after Brefeld*, 1888.)

tiny conidia (Fig. 357, 1) which are correspondingly more luxuriant in nutrient solution and sometimes surround the basidiospores with a felt (Fig. 357, 2). The conidia develop to mycelia again on suitable sub-

strates (Fig. 357, 3) (Brefeld, 1888; Dangeard, 1895; Juel, 1898). In the cultures reported by Gilbert, the daughter cells germinate directly to uninucleate mycelia; clamp connections were not observed; binucleation was first observed at the base of the fructification without discovering how it had occurred. The other species of *Dacryomyces* which have been investigated agree with *D. deliquescens;* only in *D. ovisporus* the sterigmata arise somewhat below the tip. The number of daughter cells of the basidiospores in *D. longisporus* is 12 to 15; and in *D. ovisporus* a multicellular tissue is formed by repeated transverse and longitudinal division (Fig. 357, 5).

Beyond *Dacryomyces* the development of the fructifications takes place in two directions. In some forms they gradually differentiate into head and stipe, with the hymenium limited to the head; thus in *Guepinia* (Fig. 354, 3) the fructification resembles that of *Peziza* or *Coryne*. In

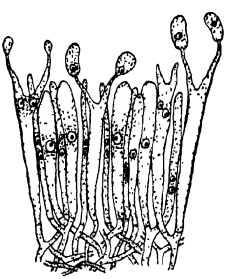


FIG. 358.—*Calocera viscosa*. Section of hymenium. (× 600; *after Dangeard*, 1895.)

Dacryomitra (Fig. 354, 5) this differentiation into pileus and stipe is still more marked. The upper surface of the head is cerebriform and the whole structure resembles a *Helvella*.

In other forms, as in *Calocera*, the development proceeds in the direction of the Cantharellales, with the hymenium completely covering the fructification. In the simpler species, as *C. cornea*, the fructifications, like those of *Eocronartium*, are small, unbranched, clavate, cartilaginous or slightly gelatinous (Fig. 354, 4); in the higher species, as *C. viscosa* (*C. flammea*), they ascend to structures which externally correspond to *Clavaria* and may only be distinguished microscopically (Fig. 354, 6). Gel formation disappears more and more, occurring only in the basal layers of the hymenium (Fig. 358). Consequently the fructifications attain a rough appearance and thus lose the last character which superficially connects them with the tremelloid *Dacryomyces*.

In the germination of the basidiospores and the form of the conidia, these three genera agree with *Dacryomyces*, but no oidia have been reported. The phylogeny of the Dacryomycetales is altogether obscure. Juel (1898) and Maire (1902) consider them to have arisen, by the sup-

pression of the septa and subsequent terminal insertion of the sterigmata, from the Auriculariaceae with which they show a remarkable correspondence in gel secretion, in method of basidiospore germination, in longitudinal orientation of the nuclear spindles and in the four basidial nuclei. Consequently, they would be the most primitive stichobasidial Autobasidiomycetes and a link between the Auriculariales and the Cantharellales. The structure and relationships of the basidia present the only objection to this concept. It is difficult to explain why such a rearrangement of the phragmobasidium should have occurred, as in the Auriculariaceae with compact gelatinous hymenia the problem of spore discharge is satisfactorily solved by the elongation of the sterigmata. Also in the Tulostomataceae, the only family in which the basidium could have arisen directly from the phragmobasidium by the suppression of a septum, the lateral insertion of the spores is retained in spite of this suppression. It is impossible to say how this rearrangement could have taken place, for no transitional forms between the phragobasidium and the *Dacryomyces* basidium are known. Similarly, there is difficulty in the extension of this assumed developmental line to the eight-spored stichobasidium of the Cantharellales, which one would have to consider as formed *de novo* from the four-spored phragmobasidium and subsequently two-spored basidium of the Dacryomycetales.

The latter difficulty was raised by the attempt on page 423 to derive the stichobasidial Holobasidiomycetes directly from the Ascomycetes, not from the sticho–Phragmobasidiomycetes. In this case, the Dacryomycetales would be primitive only in the structure of their fructifications, while their basidia would indicate an end stage like the two-spored Canthrellales. Their long sterigmata might then be considered an adaptation for penetrating the gel and, in this sense, a convergence to the sterigmata of the Tremellales, which also are broad at the base and taper upwards. A certain relationship with the Auriculariales need not be rejected; thus one may consider that both these stichobasidial orders (as indicated on p. 530) have their roots in the same Ascomycetous line and from it have retained their common primitive characteristics.

CHAPTER XXXII

AURICULARIALES

This order includes an ontogenetic series which ranges from forms without well-developed fructifications to those with characteristically gymnocarpous or angiocarpous structures. In most genera the hyphae secrete a gel and are able to withstand great changes in temperature and moisture. In some genera which lack this gel, the zeugites develop to special organs of protection called **sclerobasidia.** The Auriculariales fall more or less definitely into three families: the Auriculariaceae, Septobasidiaceae and Phleogenaceae. Their characters will appear in the following discussion, while their probable relationships are shown in the diagram on page 613.

Auriculariaceae.—This family is gymnocarpous; it develops from primitive arachnoid forms in which the basidia arise directly on the diffuse, flocculent mycelium to those with bracket fructifications, very much as we have seen in the Corticiaceae.

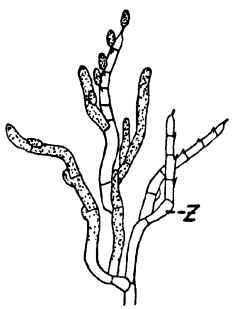


FIG. 359.—*Helicobasidium orthobasidion.* Showing clamps and basidia. (×330; *after Möller*, 1895.)

The primitive stage is suggested by *Helicobasidium* (*Stypinella*). The white, clamp-bearing hyphae intertwine to a loose felt where they radiate and end usually in small, four-celled basidia which project above the felt. The sterile mycelium of *H. purpureum* has long been known as a plant pathogen under the name *Rhizoctonia Crocorum* (*R. violaceum*) (Buddin and Wakefield, 1927). The mycelium in the vicinity of the fructification is binucleate. The fusion nucleus remains until the basidia have assumed their crozier form. Subsequent nuclear division was not observed but the basidium divides into four uninucleate cells by transverse septa. During spore formation, these nuclei divide, producing binucleate spores and mycelium. Since some uninucleate strains of *Rhizoctonia Crocorum* are known, it is not clear whether these strains belong here or whether the last nuclear division fails to occur. On germination the spores produce a branched, purplish mycelium and binucleate conidia, belonging to the Imperfect form-genus *Tuberculina.* On germination of the conidia, both nuclei pass out into the mycelium.

In the Brazilian *H. orthobasidion,* the hyphal cell which bears the basidium (Fig. 359, *z*) shows a tendency to assume a definite form when

it approaches the other hyphal cells. It becomes shorter and stouter than the others, collecting the protoplasm of the cells immediately behind it and passing this into the basidium. Close below this appears the usual branch which projects over the empty basidium and itself develops to a basidium.

Platygloea (*Achroomyces*) represents the next step in the formation of simple resupinate fructifications. The hyphae secrete a gel, hence the texture is waxy to gelatinous, often convoluted when fresh. The basidia are united into a loose hymenium, interrupted by paraphyses (?). As in *H. orthobasidion*, so in *Platygloea nigricans* (*Achroomyces Tiliae*), the probasidium, in which nuclear fusion occurs, remains in the mature basidium, recognizable as a slight swelling (Neuhoff, 1924) similar to that shown in Fig. 359, *z*. The sterigmata of the lower basidial cells continue their growth until they have reached the surface of the gel and then cut off their spores, so that the latter do not adhere to the gel. In *P. Lagerstroemiae*, the basidia begin to collapse and become distorted as the basidiospores form. The basidiospores germinate in nutrient solutions with sprout cells or secondary spores which are similar in form to the basidiospores, but smaller (Möller, 1895; Coker, 1920). In *P. caroliniana* there are no sterile hyphae in the hymenium. Swellings at the base of the basidia have not been reported in the North American species.

In *Eocronartium*, the fructifications become more definite in form, being cylindrical or clavate in *E. muscicola*, (Fig. 360, 1, *sp.*) a perennial parasite on mosses in Europe and North America (Fitzpatrick, 1918). The hyphae penetrate the whole stem, but haustoria and clamp connections are not reported. The origin of the binucleate cells is unknown. The nuclei divide conjugately, with the spindles often perpendicular to the axis of the hypha. Shortly before the formation of the fructification, the intramatrical hyphae emerge between the folded leaves, intertwine and elongate to a cylindrical fructification. In case the sporogonium of the host is already formed, it is surrounded by hyphae. At the surface of the fructification, in the terminal cells of the hyphae, the two nuclei approach and fuse (Fig. 360, 4). The zeugites (Fig. 360, 5, *z*) swell slightly and develop to long basidia (Fig. 360, 6 to 13) bearing four basidiospores on long sterigmata. In nutrient solutions they germinate with germ tubes whose cells are uninucleate. Perhaps plasmogamy occurs early, but it was not observed.

In *Auricularia*, the highest member of this family, the fructification is a broad, bilateral bracket. The cosmopolitan *A. Auricula-Judae* is irregularly lobate, sometimes conchiform or auriform. In fresh condition, it is more or less gelatinous or cartilaginous, drying hard and horny, to revive again when moistened, as in the Marasmieae and Schizophylleae of the Agaricales. The hymenium and the sterile surface is smooth or slightly rough in this species, but in tropical species the hymen-

ium becomes reticulate until it is almost merulioid, while the sterile surface may be strigose to tomentose (Fig. 361).

As usual, the hyphae of the fructifications are binucleate; the basidia are united in a palisade and at their base may show the place of nuclear fusion by a slight swelling. They are entirely imbedded in a gel (Fig. 362, 1) and, as those of *Platygloea*, elevate their spores on long sterigmata to the surface. At germination, the basidiospores may be abjointed

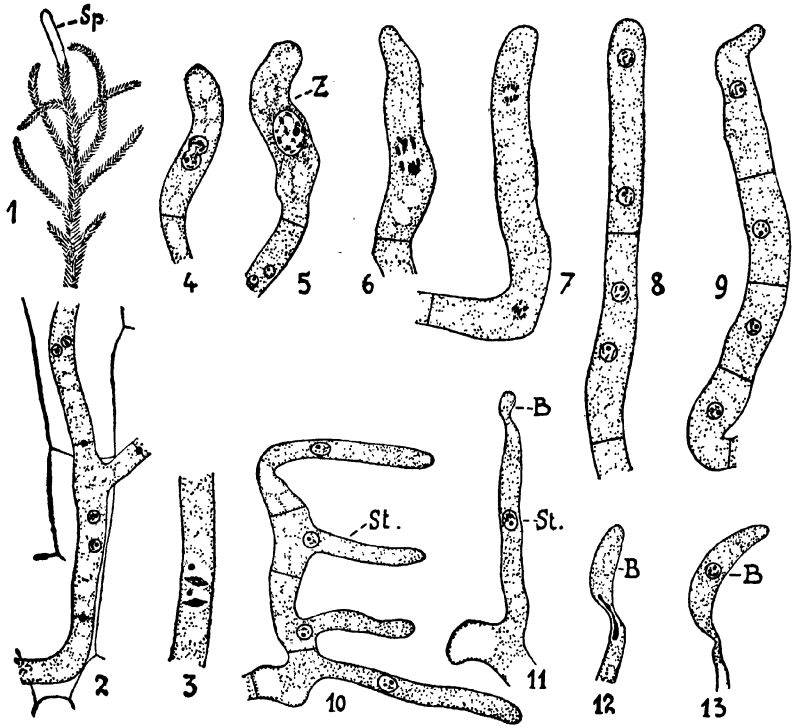


FIG. 360.—*Eocronartium muscicola*. 1. Moss with sporogonium, *Sp*. 2, 3. Hyphae in host tissue. 4 to 9. Development of basidia. *Z*, zeugite. 10, 11. Formation of basidiospores. 12. Migration of nuclei into basidiospores, *B*. 13. Basidiospore before abscission. (1, natural size; 2 to 13 × 1,400; *after Fitzpatrick*, 1918.)

into two daughter cells which may again become septate. If germination occurs in water, these daughter cells develop short, branched germ tubes which cut off masses of small, uninucleate, falcate conidia on short sterigmata (Fig. 362, 2 to 4). If germination occurs in nutrient solutions, conidial formation may at first be retarded, and the basidiospores develop luxuriant mycelia, on which later may occur coremia of ramose conidiophores bearing masses of falcate conidia at their tips (Fig. 362, 6). The

conidia develop to mycelia in nutrient solutions (Brefeld, 1888; Möller, 1895; Istvanffi, 1895; Sapin-Trouffy, 1896; Juel, 1898; Maire, 1902).

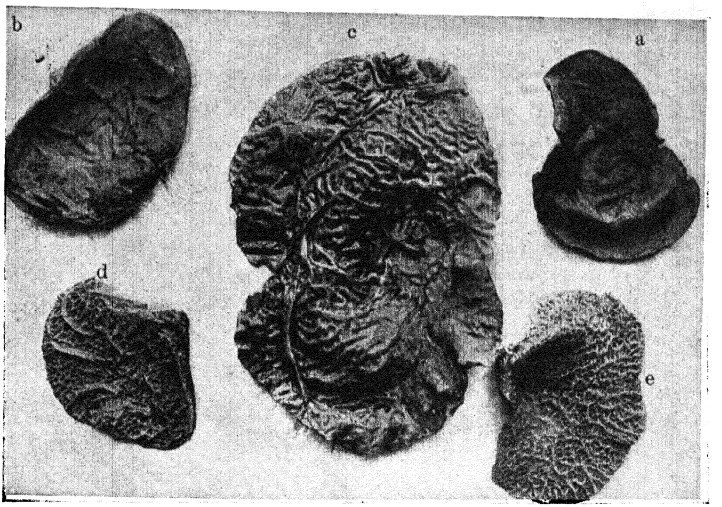


FIG. 361.—*Auricularia Auricula-Judae.* Five fructifications showing transition from smooth to faveolate hymenium. (× ½; *after Möller*, 1895.)

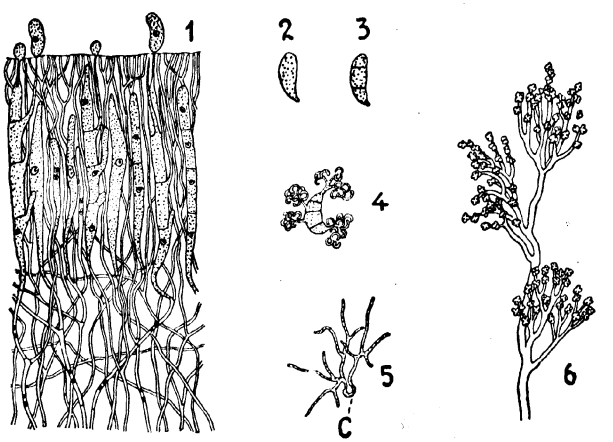


FIG. 362.—*Auricularia Auricula-Judae.* 1. Section of hymenium. 2 to 4. Germination of basidiospores with falcate conidia. 5. Falcate conidium, *C*, germinating to slender mycelium. 6. Conidiophore from a coremium of falcate conidia. (1 to 5 × 280; 6 × 66; *after Sappin-Trouffy*, 1896, *and Brefeld*, 1888.)

Septobasidiaceae.—This family includes four genera which are not very closely related, but present a series with increasing differentiation of the zeugites.

Iola, mostly parasitic on moss sporophytes, continues the tendency of *Helicobasidium* and *Platygloea nigricans* to store up reserves in the zeugites which are developed to characteristic organs called probasidia. The mycelium grows through the cap of the sporogonium, forming a thick felt between cap and capsule and then penetrates the interior. The hyphae are binucleate, septate and without clamps. At the surface of the sporogonium (Fig. 364, 8, *Sp*) they form a felt which is relatively loose in the Brazilian *I. Hookeriarum* (Möller, 1895). In *I. javensis* (Gäumann, 1922), the hyphae are imbedded in a gel forming a small fructification like a drop of slime on top of the sporogonium (Fig. 364, 7, *Sp*). The hyphae are slightly sinuate, being quite parallel to each other in the

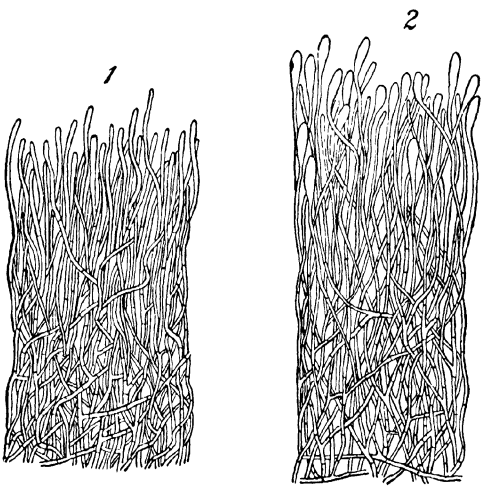


FIG. 363.—*Iola javanensis*. 1. Section of young hymenium. 2. Older stage, showing the beginning of the formation of probasidia. (× 375; *after Gäumann*, 1922.)

extramatrical part in Fig. 363. Their ends become clavate, the two nuclei approach and fuse (Fig. 364, 2 and 3).

The zygote nucleus remains a short time in a resting state, then passes over into the prophase. It migrates to the tip of the probasidium and begins synapsis. Meanwhile a parallel branch is formed below the primary probasidium, the dicaryon of the uppermost hyphal cell, the subterminal cell, migrates to the top of the cell and divides conjugately. One-half the daughter nuclei slip into the branch which again swells to a probasidium and pushes aside the primary probasidium. The other half remain in the hyphal cell where the formation of new probasidia is repeated (Fig. 364, 3 to 5), finally resulting in the structure shown in Fig. 364, 1; thus the whole development of probasidia rests in the dicaryon of the subterminal cell.

While the younger probasidia continue developing, the older ones germinate to basidia which remain enucleate for a long time (Fig. 364, 5 and 6, *B*). When they have reached approximately three-fourths of their final length, the diploid nucleus migrates into them and divides normally into four daughter nuclei which slip out into the basidiospores. In *I. Hookeriarum*, the sterigmata are of unequal length and elevate the

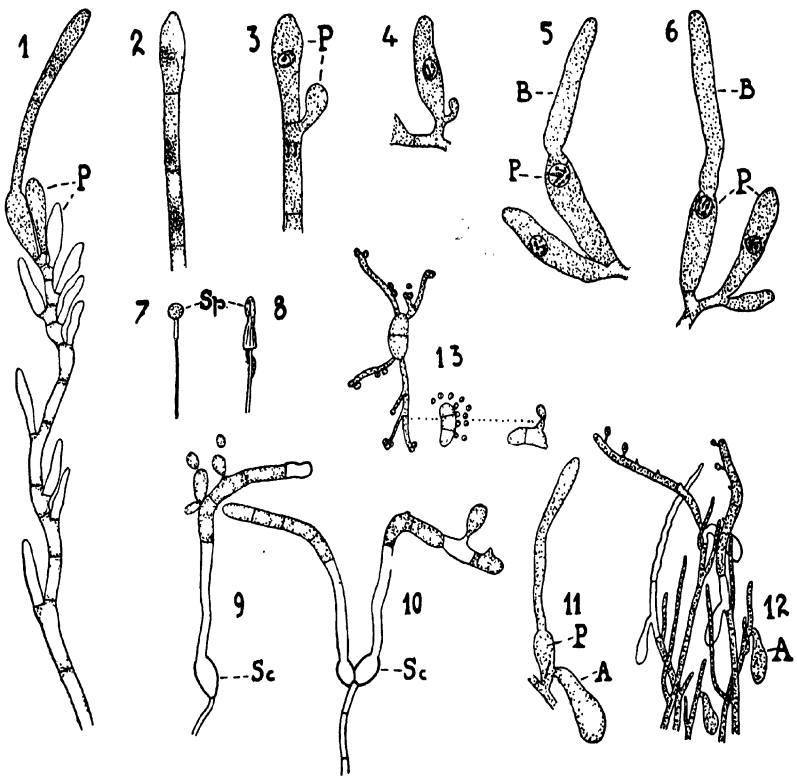


FIG. 364.—*Iola javanensis*. 1 to 6. Development of probasidia. 7, Spherical fructification, *Sp*, on sporogonium of moss (natural size). *Iola Hookeriarum*. 3. Irregular fructification of diplont of moss (natural size). *Cystobasidium Lasioboli*. 9, 10. Germination of sclerobasidia, *Sc*. *Saccoblastia ovispora*. 11, 12. Development of basidia. 13. Germination of basidiospores. (× 150; *after Gäumann*, 1922; *Lagerheim*, 1898; *and Möller*, 1895.)

spores above the hymenium, while in *I. javensis* the basidium projects above the gel which only extends to the tops of the probasidia. The basidiospore germinates with a uninucleate secondary spore; further stages of germination and the genesis of the dicaryon are unknown.

Perhaps the probasidia, filled with reserve material for the formation of basidia, have an ecological function as well as their biological function

as zeugites. In the case of *I. javensis* of the damp mountain forests of West Java, after an hour in free air with a relative humidity of 70 per cent and a temperature of 26° C. in the shade, the fructifications collapse. Returned to a crystalizing dish saturated with moisture, they resume somewhat the former appearance in the course of a week. If the relative humidity in the forest does not drop below 90 per cent, that prevalent in the rainy season on the moss carpet between the undergrowth, the conditions of life are fulfilled. If the stores of nutrients which on the advent of high humidity may be used for basidial formation are not collected in the probasidium during a relative drought, the whole life process is at a standstill and the first basidia do not appear until 4 to 7 days after the resumption of growth. Hence in this species, the probasidia are not in a position to carry the fungus over unfavorable conditions as we shall find in subsequent groups. The hyphae within the sporogonium alone remain intact.

A second factor is air temperature. The lower limit for basidial formation lies at 15° C., the optimum between 18° and 26° with a maximum at 30°. Measurements taken under natural conditions have shown that only in the late morning are these limits exceeded and that after sunset the temperature again falls below the minimum. New basidia may only be formed during a short time. Therefore it appears that the probasidia are storage organs in which reserves are accumulated and meiosis occurs, so that when temperature relations are favorable, basidia may be formed more rapidly. If the humidity is sufficient, and the temperature below 15°, only preparation occurs, while as soon as the temperature rises above this limit, the basidium is protruded above the gel. The function of protection is probably assumed by the gel, since fructifications containing a gel are usually very resistant to cold.

In *Cystobasidium,* which lacks a gel, the zeugites develop as organs of protection. *C. Lasioboli* (Lagerheim, 1898) forms arachnoid covering on the fructifications of *Lasiobolus.* Occasionally the hyphae have clamp connections. On short branches they form probasidia whose walls are considerably thicker than those of the basidia which arise from it or than those of the hyphae (Fig. 364, 9 and 10, *Sc*). The basidiospores germinate in nutrient solutions by "sprout" conidia. The probasidia of this species unite in themselves the ecological functions of resting organs and of protective organs. Since they are encysted they will be called **sclerobasidia** and are homologous with the teliospores of the Uredinales.

In *Saccoblastia,* whose only carefully studied species is *S. ovispora* (Möller, 1895; Coker, 1920) found in Brazil and North Carolina on the bark of trees, the mycelium forms a delicate, almost transparent covering. On this there project somewhat thinner hyphae whose terminal cells, as in *Iola,* occasionally swell slightly (Fig. 364, 11, *p*), and form lateral,

pyriform outgrowths, which bend down on account of their weight (Fig. 364, 11 and 12, *A*). During the development of the basidium, the content of this sac passes into it, whereupon the basidium is abjointed and forms basidiospores. As in *Iola*, the subterminal cell develops a new probasidium. The basidiospores develop, with or without previous septation, to secondary spores or form a gelatinous mass of small conidia, surrounded by a viscid gel (Fig. 364, 13). A cytological study of this species is needed for the interpretation of this storage organ which is unknown in other groups of fungi.

Septobasidium also lacks the gel, and shows an increasing differentiation of zeugites. It is chiefly a tropical genus, although a few species

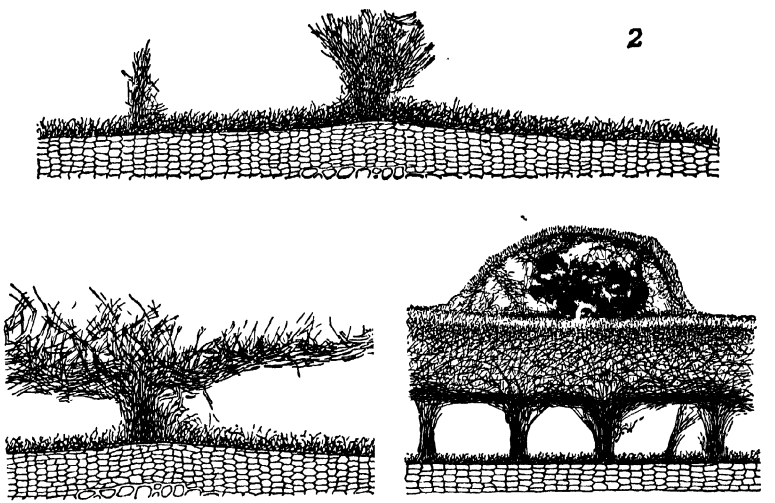


FIG. 365.—*Septobasidium bogoriense*. *A*. Section of outer growth zone of crust. *B*. Hyphae developing pillars. *C*. Section of mature crust, stimulated by particles of earth to new growth. (× 110; *after Gäumann*, 1922.)

occur as far north as southern Canada. As far as they are known, they grow either saprophytically or epiphytically on the secretions of scale insects (Petch, 1911; Burt, 1916) and only with difficulty on the trunks and twigs of trees. The hyphae are hyaline when young, becoming yellowish to dark brown in age.

The species of *Septobasidium* may be separated into two groups which would probably be given generic rank, were it not for such transitional forms as *S. cirratum*. In the more primitive group, the fructification is a loose, arachnoid, flocculent crust, with either unlimited growth at the margin, or restricted growth, resulting in reticulate or sinuously divided fructifications, giving the appearance of foliose lichens. The

basidia are formed in the uppermost portion of the crust from pyriform to spherical probasidia, which are either terminal on the ends of hyphae or irregularly borne on lateral branches of more or less coiled hyphae. In *S. frustulosum*, the probasidium becomes septate and functions as a basidium, as do the teliospores of the Coleosporiaceae in the next order (Burt, 1916). In *S. pinicola* on *Pinus Strobus* and *P. monticola*, the probasidia are apparently at the same stage of development as in *Iola*, since the walls are not thickened and the basidium develops within a short time (Snell, 1922). In *S. retiforme* and *S. frustulosum*, the probasidia are colored brown, but no statement is made as to the thickness of the wall.

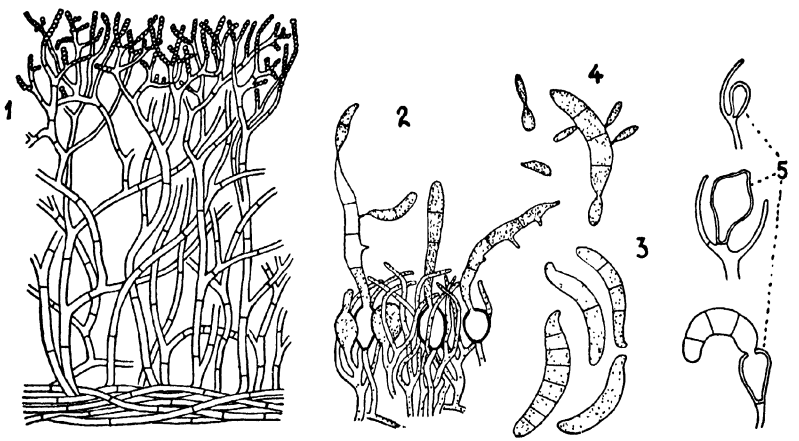


FIG. 366.—*Septobasidium albidum*. Group of conidia resembling *Torula*. (× 400; *after Patouillard*, 1913.) *Septobasidium pseudopedicellatum*. 2. Section of upper portion of crust (× 360). 3, 4. Germinating basidiospores. (× 720; *after Coker*, 1920.) *Septobasidium pedicellatum*. 5. Development and germination of probasidia. (× 260; *after Patouillard*, 1892.)

The more highly differentiated group of species produce a layer of tissue next the substrate, from which rise hyphal pillars which support the outer layer bearing the hymenium (Fig. 365). *S. cirratum* forms a transition from the primitive group, since the pillars are of variable diameter and composed of loosely intertwined hyphae. In many species of this group the wall of the probasidium is thickened, and in *S. castaneum* also slightly colored, hence the zeugites might be called sclerobasidia (Fig. 366, 2 and 5).

The basidiospores germinate directly to secondary spores, rarely to mycelia. In *S. pseudopedicellatum* and *S. retiforme*, they divide into as many as eight daughter cells before germination (Fig. 366, 3 and 4). These cells produce elongate sprout cells (Coker, 1920; C. W. Dodge, unpublished observations). In *S. retiforme* the basidium falls from the probasidium

before spores are produced on the lateral sterigmata, reminding one of the conditions found in some smuts. In *S. Michelianum* (Kühner, 1926) the uninucleate basidiospores germinate with a short sterigma which bears a secondary spore only slightly smaller than itself. This becomes three to six septate and produces one to two very small, ellipsoidal conidia from each cell. The binucleate basidiospores form a septum between the nuclei then germinate as above.

The morphological significance lies in the increasing differentiation of the zeugites which, here for the first time in semiparasitic forms, attain the height of development of teliospores. Consequently *Cystobasidium* and *Septobasidium* form an important approach to the Uredinales.

Conidial fructifications have only been observed in *S. albidum* from the East Indies (Patouillard, 1913). The hyphal tips are differentiated into hyaline, later colored oidia (Fig. 366, 1).

Phleogenaceae.—As in the other families of the Auriculariales, this family begins with gymnocarpous forms, although here the higher

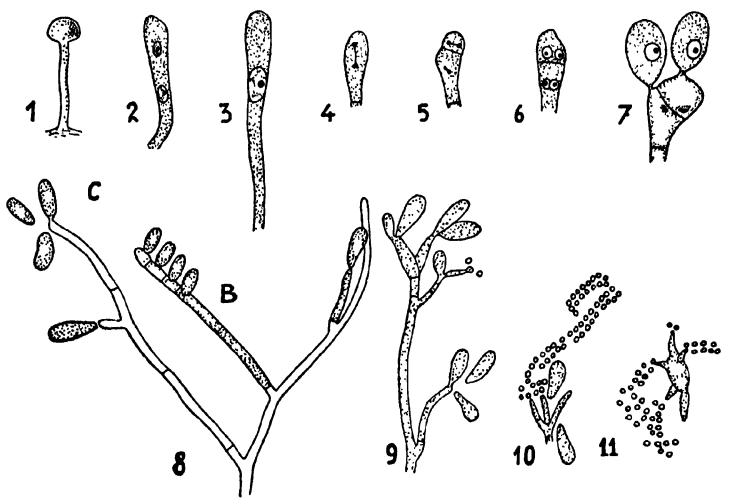


FIG. 367.—*Stilbum vulgare*. 1. Fructification. 2 to 7. Development of basidia. *Hoehneliomyces delectans*. 8. First basidium appearing on conidial hyphae. *C*, conidium; *B*, basidium. 9, 10. Macro- and microconidia, the latter catenulate. 11. Germination of basidiospore with short hyphae, producing catenulate microconidia. (1 × 33; 2 to 7 × 1,320; 8 to 11 × 330; *after Juel*, 1898, *and Möller*, 1895.)

members are angiocarpous. The basidia arise irregularly within definite layers which correspond to the gleba of the angiocarpous Basidiomycetes. The basidia lack sterigmata.

In *Stilbum vulgare* (Juel, 1898) the fructification is scarcely more than a well-developed coremium, with the erect hyphae held together by

a gel. The cells are binucleate, the terminal cells become pyriform, the dicaryon fuses, the diploid nucleus divides twice with more or less longitudinal spindles. The basidia are two celled. After the first division a single septum forms and one nucleus slips into the basidiospore while the other degenerates (Fig. 367, 2 to 7).

Pilacrella Solani is rather better developed, the caps becoming fleshy discs while the fertile layer contains long sterile periphyses which extend above the basidia.

Hoehneliomyces shows the step from gymnocarpous to angiocarpous development. *H. delectans* (*Pilacrella delectans*) on fallen leaves and

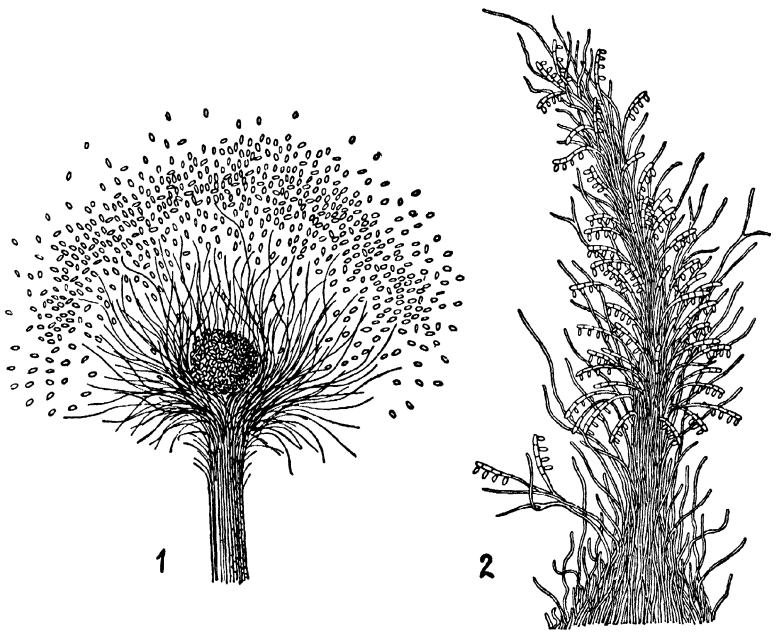


FIG. 368.—*Hoehneliomyces delectans*. 1. Head of fructification. 2. Fructification in artificial culture before formation of head. (1 × 46; 2 × 6; *after Möller*, 1895.)

stems of *Euterpe oleracea* in Brazil (Möller, 1895), forms a small watery irregular knob of hyphae on the substrate. From this arises a hyaline stipe formed of parallel hyphae which grow out below in all directions, giving the stipe a hairy covering (Fig. 368, 1). At the base of the cap, the peripheral hyphae are much branched, growing outward, then bending toward each other like a calyx. The central hyphae of the stipe, within this calyx, develop basidia at their tips. The basidiospores are not

discharged but collect in a shining white knob, supported by the "calyx." They germinate easily in nutrient solution (Fig. 367, 9 to 11). Besides, a large number of microconidia may be formed, each of which is surrounded by a thin gel. They do not germinate beyond a slight swelling. The hyphae from germinating basidiospores form coremia (Fig. 368, 2), basidial formation is limited to the top of the coremium, and fructifications result similar to those found in Nature. In the Javan *Hoehneliomyces javanicus* (Weese, 1920) the "calyx" is better developed than in *H. delectans* with its hyphae adhering to form a definite peridium around the basidial head. Here we have an angiocarpous fructification.

In *Phleogena faginea* (*Pilacre faginea, P. Petersii*), the highest member of the series (Fig. 369), development is entirely angiocarpous. This species is found in late fall and winter on *Fagus*, occasionally on *Acer* and *Carpinus* (Brefeld, 1888; Istvanffi, 1895; Shear and B. O. Dodge, 1925).

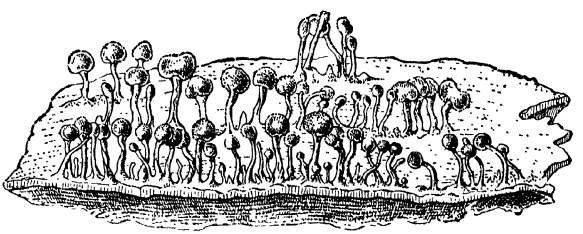


FIG. 369.—*Phleogena faginea*. Habit of fungus on beech bark. (Natural size; *after Brefeld*, 1888.)

Its stipe consists of a bundle of parallel hyphae. In the fundament of the head, the hyphae radiate and branch repeatedly, the branches becoming very small. At a certain stage they begin to bend inwards at the top of the pileus, forming the so-called peridium (Fig. 370, 2 and 3). This process proceeds basipetally. Within this zone, there arise loose coremia of clamp-bearing hyphae whose tips are transformed into basidia. In contrast to *Pilacrella* and *Hoehneliomyces*, the whole fructification consists of uniform hyphae, the same hyphae which form the stipe, intertwine to form the peridium and later the basidial branches which fill the interior of the fructification (Fig. 370, 4).

When the spores are mature, the basidia and basidial branches shrivel, leaving only a mass of spores. The peridium, thanks to the helical involutions of the hyphae, winters over and disintegrates in the spring with anemochoric spore dispersal. The spores are thick-walled, light yellow to dark brown, possessing thin germ pores. They germinate to coarse brown, clampless primary mycelia which cut off brown, uninucleate conidia similar to species of *Rhinotrichum*. These germinate to

delicate, pure white, secondary mycelia, which become binucleate by extensive clamp formation. In the basidium, after the first division of

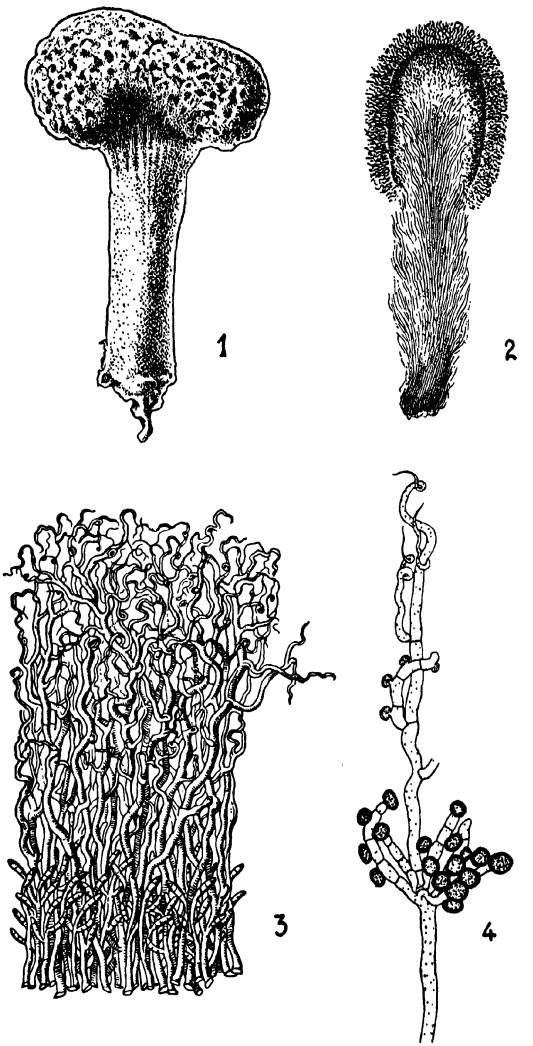


FIG. 370.—*Phleogena faginea*. 1. Mature fructification. 2. Section of young fructification forming the peridium. 3. Section of peridium with basidia below. 4. Loosely intertwined hyphae with basidia. (1 × 10; 2 × 16; 4 × 500; *after Brefeld*, 1888.)

the fusion nucleus, a wall is formed before the second division. Each of the four cells of the basidium produces a single uninucleate spore.

CHAPTER XXXIII

UREDINALES

The Uredinales, frequently called Uredineae or rusts, form a parasitic branch of the Auriculariales; as in the latter, the zeugite develops to a special organ which is encysted and acts as a resting spore in the higher forms. They differ from the Auriculariales, however, by the higher differentiation of these resting spores, by the varied types of other spore forms and by the lack of fructifications. They include three thousand species which are exclusively parasitic on cormophytes. Saprophtyic forms or forms cultivatable on artificial media, are still unknown.

The mycelium consists of regularly septate, ramose hyphae, whose cells, particularly when young, contain numerous orange-colored drops of oil. Normally it grows intercellularly and sends allantoid, seldom branched or knotted, haustoria into the host cells which are not killed but only robbed of part of their substance. In many species, the mycelium is limited to a small area near the place of infection; these species are annual; in others, outside of the tropics, it penetrates the whole host or a large part of it, overwinters in the perennial parts and grows again in the following spring. The mycelium of these species is perennial; it produces many kinds of malformations, sparse growth of the whole plant, enlargement or reduction of leaf surface, suppression or stunting of the floral parts, witches' brooms, etc. On *Urtica parviflora*, the hypertrophies which are produced by *Puccinia Caricis* accumulate in such large quantities that in central Asia they are eaten by the natives. In one case, in the Javan *Goplana mirabilis* on the leaves of *Meliosma*, extramatrical mycelium has been demonstrated. The cells of the hyphae are uninucleate in some portions of the life cycle, in others wholly binucleate; the haustoria are at times four nucleate. Occasionally clamp connections appear on the hyphae, as in the Auriculariaceae (Voss, 1903).

There are five spore forms: pycnospores, aeciospores, urediniospores, teliospores and basidiospores. We shall discuss them in the order they usually appear in nature.

The first spore forms visible in spring are the pycnospores (also known as pycnidiospores, or spermatia). They arise exclusively in uninucleate mycelium and in certain sori, pycnia (pycnidia or spermogonia). These lie either between the epidermis and cuticle, and are then more or less flat (Fig. 371, 2), or they are hypodermic, and are then often sunk into the host tissue as spherical or perithecial-like structures.

They develop as follows: The hyphae, which penetrate to the surfaces from the intercellular spaces intertwine to form a thin pseudoparenchymatous stroma. On its surface the hyphae grow perpendicularly to the surfaces of the leaves or radially, toward a common center, and form a layer of slender parallel hyphae (Fig. 371, 3) which generally have terminal, somewhat annular, colored thickenings. Above this ring, a young oval pycnospore develops. Meanwhile the nucleus has divided, one daughter nucleus migrates through the structure into the young spore which is separated above the thickening

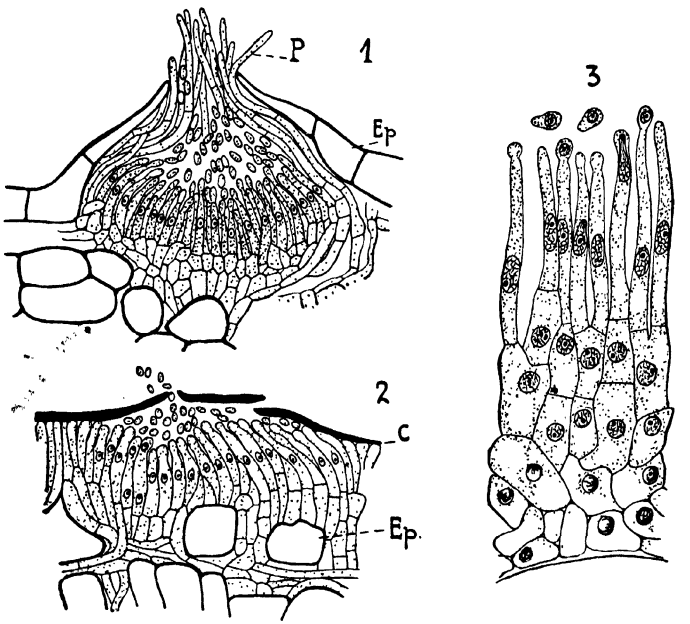


FIG. 371.—1. *Gymnosporangium clavariaeforme.* Section of a pycnium on leaf of *Crataegus* (× 345). 2. *Phragmidium violaceum.* Pycnium on *Rubus* with ruptured cuticle (× 440). 3. *Cronartium ribicola* portion of pycnium (× 1,160). *P*, paraphyses; *Ep*, epidermis; *C*, cuticle. (*After Blackman*, 1904, *and Colley*, 1918.)

by a septum and which then falls off. The other remains behind in the basal cell and divides repeatedly, forming many successive spores. The periphery of the whole sorus is surrounded by a ring of periphyses (in systematic works often called paraphyses) which have arisen by the elongation of the outer cells of the stroma. They intertwine in a dome over the fertile tissue and later by their pressure, rupture the epidermis.

In the primitive Pucciniastreae, the periphyses are absent, the cuticle or epidermis of the host being the only covering of the sorus. At first this is often penetrated by a small pore through which the pycnospores (spermatia) are extruded. Later the whole cuticle or epidermis may

rupture, laying bare the sorus (Hunter, 1926). In *Calyptospora Goeppertiana*, the pycnia are formed normally but the pycnospores regularly abort. In *Gallowaya pinicola* (B. O. Dodge, 1925) on *Pinus virginiana*, vestigial pycnia (spermogonia) are formed but they fail to rupture the overlying tissue or to form pycnospores (spermatia).

Pycnospores are ovoid or spherical, very small (2 to 4μ) or, if bacilliform, up to 1.6 by 9μ; their membrane is hyaline and smooth; their content poor in cytoplasm and reserve materials; the nucleus is comparatively large, sometimes occupying two-thirds of the cell volume. They accumulate as a slimy mass in the cavity formed by the periphyses and are repeatedly extruded; in some species, as *Cronartium ribicola*, *Endophyllum Sempervivi* and *Puccinia obtegens* (*P. suaveolens*), they have a sweetish odor, in *Gymnoconia Rosae*, an offensive odor. Their further development is unknown. In some species, *e.g.*, *Phragmidium violaceum*, they appear to degenerate early (Blackman, 1904); in others, as *Cronartium ribicola*, they appear to be normal (Colley, 1918). In any case, they seldom germinate and when they do form a short germ tube, it is not capable of producing infection.

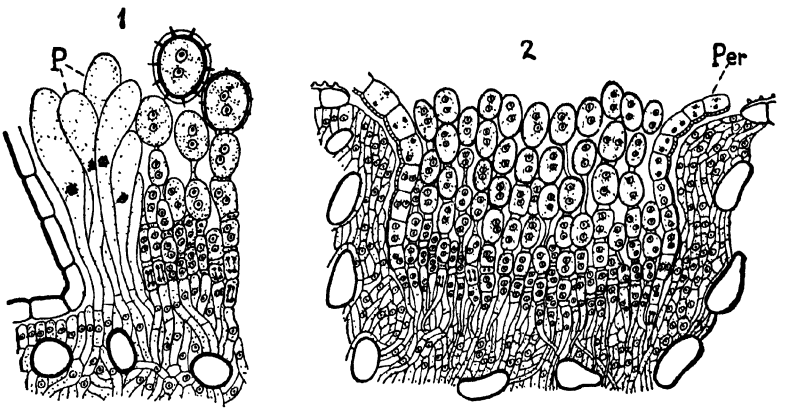


FIG. 372.—Types of aecia. 1. Caeoma of *Phragmidium Rubi*. *P*, paraphyses. 2. Aecidium of *Uromyces Erythronii*. *Per*, peridium. (1 × 400; 2 × 300; *after Sappin-Trouffy*, 1896.)

Simultaneously with the pycnospores or shortly thereafter, a second spore form, the aeciospores, usually develops in special sori, the **aecia**, on the uninucleate mycelium. These belong to two types: the **caeoma**, which is usually placed directly under the cuticle or epidermis, is broad and flat, naked or covered by periphyses (in the Uredinales, usually called paraphyses, Fig. 372, 1). After its formation it is able to spread laterally and is consequently indefinite in form. In the higher type, the **aecidium** (or cup type) is placed in the host tissue, several cell layers deep; it is spherical or ellipsoidal and always covered by **pseudoperidium**, also

called peridium for short. A further development in breadth is unknown in them; in many cases, however, no sharp difference between caeoma and aecidium can be drawn, for species with peridia rudimentary or almost lacking appear in groups with well-developed peridia.

The development of the caeoma will be first described, *e.g.*, *Phragmidium violaceum* (Blackman, 1904; Welsford, 1915), *P. speciosum* (Christman, 1905), *P. disciflorum* (*P. subcorticium*) (Mme. Moreau, 1914) *Gymnoconia Peckiana* (Christman, 1905; Olive, 1908; Kursanov, 1910), *Melampsora Rostrupi* (Blackman and Fraser, 1906), *M. Lini* (Fromme,

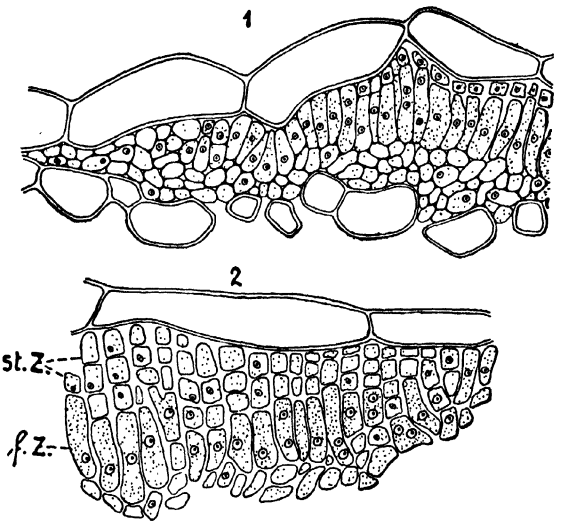


FIG. 373.—*Phragmidium disciflorum*. 1, 2. Development of caeoma. *St. Z.*, sterile cells; *F.Z.*, fertile cells. (1 × 535; 2 × 670; *after Moreau*, 1914.)

1912) and *M. reticulata* (Lindfors, 1924). The first indication of the fundament consists in an accumulation of intercellular hyphae between the epidermis and mesophyll. The cells of the hyphal knot next the epidermis elongate perpendicularly to it and lie close together, forming a subepidermal palisade layer. Each divides into a small sterile cell above and a large fertile cell below (Fig. 373). Where there is enough room, *e.g.*, in the spaces between the epidermal cells, the fertile cell repeats this division, so that a chain of as many as four sterile cells may result; in *Melampsora Lini* there are usually two, and in *Melampsora Rostrupi* many sterile cells. The nucleus of the sterile cell remains small, degenerates and disappears. This is followed by the gradual degeneration of the sterile cells themselves.

Meanwhile, proceeding from the middle toward the margin, the walls between two fertile cells dissolve, the protoplasts fuse and a large, binu-

cleate, fusion cell is formed (Fig. 374, 1 to 3). Under exceptional circumstances more than two fertile cells fuse, producing a multinucleate fusion cell. Since both fertile cells in Fig. 374, 1 to 3, are equal in form and position, the plasmogamy is isogamous. There also appear in the same sorus many deviations from this isogamous type. Thus cells of different ages may copulate, *e.g.*, one of these may have cut off the sterile

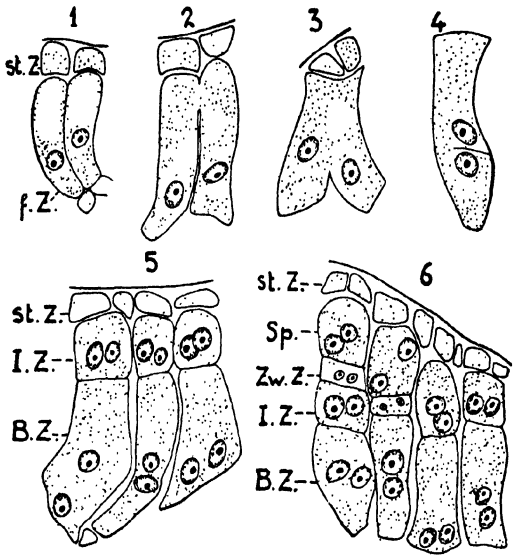


FIG. 374.—*Phragmidium disciflorum*. Development of aeciospores. 1 to 3. Fusion of basal cells. 4. Fusion of superimposed cells. 5, 6. Development of aeciospores. (× 1,130; *after Moreau*, 1914.)

cell before the other; their position may be different (one somewhat higher than the other); and, finally, the septum may be only incompletely dissolved so that there may be only a pore through which the nucleus of one cell passes into that of the other. Where these forms appear singly, they may have been caused as pathological processes or as artifacts by the uneven penetration of the fixative; in other forms, *e.g.*, *Phragmidium violaceum* in which they appear normally, their heterogamous nature may not be contested. Furthermore, frequently instead of the septum between two basal cells, the septum between one basal cell and the underlying hyphal cell is dissolved (Fig. 374, 4) or the wall between a basal cell and a cell of the neighboring mycelium or, finally, the wall between any two mycelial cells is dissolved. Thus plasmogamy may be autogamous or pseudogamous.

The fusion cell elongates in the direction of the epidermis; its dicaryon passes to the tip and divides. The fusion cell then divides, as in the earlier cells, into a small apical and large basal cell (Fig. 374, 5, *iz* and *bz*). The basal cell elongates and repeats the above process so that a chain of binucleate cells arises; occasionally a basal cell may fork and form several, similar, parallel chains; perhaps in the multinucleate cells, the binucleate condition may again be attained. By the increasing pressure of the growing chain, the remains of the sterile cells are pressed together into a formless mass.

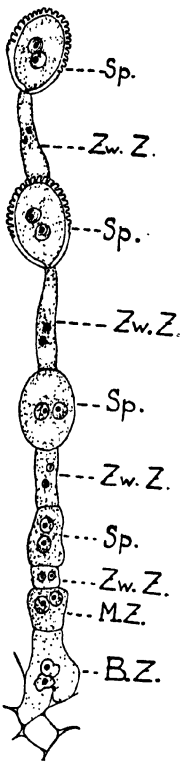


FIG. 375.—*Cronartium ribicola.* Section of aeciospores in chain. *Sp*, aeciospores; *Zw. Z.*, intercalary cells; *M. MZ.*, aeciospore mother cells; *B.Z*, basal cell. (× 560; *after Colley*, 1918.)

These binucleate cells thus cut off, are called initial cells or aeciospore mother cells. After their nuclei have completed a conjugate mitosis, each divides by septal formation into a large terminal and small basal cell. The larger cell rounds up, the walls become sculptured and thickened and it is called an **aeciospore** (Fig. 374; 6, *sp*). The smaller intercalary cell (Fig. 374, 6, *zw. z.*) disintegrates and disappears, usually before the maturity of the sorus; biologically it fulfills the function of a disjunctor, since by its degeneration, the aeciospores are loosened from the chain for further dispersal. Under favorable conditions, one finds in the young sorus a crushed sterile cell above and a free aeciospore below (Fig. 375), then aeciospores with intercalary cells, aeciospore mother cells and, at the base, binucleate basal cells in full activity. Finally the epidermis is ruptured by the pressure of the sorus and the aeciospores escape into the free air.

In the aecidium, the fundament of the sorus is a knot of plectenchyma which is sunk several layers of cells deep into the host tissue, in contrast to the position of the caeoma. In *Puccinia Pruni-spinosae*, the hyphae of the upper half of the knot grow further into the host tissue. The cells of the knot are isodiametric and about equal in size. At the margin, a peridium of 5 to 6 layers of thick-walled cells is formed. Further differentiation of the knot varies and may be classified under four types, represented by *Puccinia Mariae-Wilsoni* (*P. claytoniata*), *Uredinopsis americana* (*U. mirabilis*), *Puccinia Violae* and *Endophyllum Sempervivi.*

In the *Puccinia Mariae-Wilsoni* type, (Fromme, 1914), to which conform *P. Poarum*, *Uromyces Poae* (Blackman and Fraser, 1906), *Cronartium*

ribicola (Colley, 1918), *C. Comptoniae*, *C. pyriforme* (Adams, 1919), *Uromyces Caladii* (Christman, 1905; Fromme, 1914), *Puccinia Caricis* and *P. Pruni-spinosae* (Kursanov, 1922), the hyphae of the knot are arranged

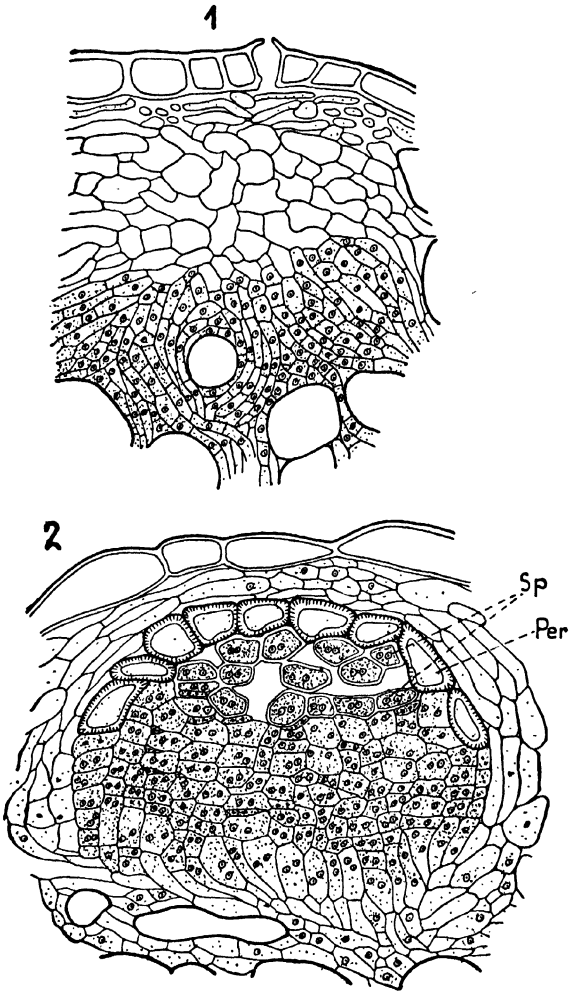


FIG. 376.—*Uromyces Poae*. 1. Young aecidium. Fertile cells above and sterile degeneration cells below. 2. Immature aecidium with peridium, *Per*, and immature aeciospores, *Sp*. (× 415; *after Blackman and Fraser*, 1906.)

in a more or less palisade-like structure and are usually perpendicular to the plane of the epidermis, in a few species pointed toward the middle of the top. The terminal cells (in *P. Pruni-spinosae*, a few intercalary cells)

swell greatly, form a loose pseudoparenchyma poor in cytoplasm, and begin to degenerate slowly (Fig. 376, 1). This swelling and degeneration of the cells proceeds basipetally, until the pseudoparenchyma includes two-thirds to three-fourths of the knot and only 4 to 5 of the basal cells of the hyphae remain. These are filled with cytoplasm and are apparently richly nourished at the expense of the disintegrating terminal cells. Between each cell of a hypha and a cell of a neighboring hypha, follows a fusion of protoplasts, as in the caeoma, by the solution of the separating wall at first in the center, later in the periphery of the sorus. Usually only one cell of a hypha takes part in plasmogamy; but all are potentially capable, since the fusion cells lie scattered irregularly (*i.e.*, at unequal heights) over the basal tissue and it is impossible to predict which cells are active. In addition, two cells lying one above the other may copulate with the same hypha. The further development of the fusion cells, the cutting off of the initial cells and their differentiation into aeciospores and intercalary cells, takes place in the same manner as in the caeoma. The growing spore chains push the pseudoparenchyma in front of them and press against the epidermal layer of the host tissues.

The type of *Uredinopsis americana*, to which belong *Thekopsora Vaccinïorum* (*Pucciniastrum Myrtilli*) (Adams, 1919) and *Gymnosporangium juniperinum* (Kursanov, 1922), resembles *Puccinia Pruni-spinosae* in the differentiation of the hyphal knot. As in the latter, the intercalary cells swell up; over the degenerated, gelatinous pseudoparenchyma there lies another layer of compact vegetative tissue which separates the pseudoparenchyma from the host tissue.

The third type, which includes *Puccinia Violae* (Fromme, 1914; Mme. Moreau, 1914; Kursanov, 1922), *P. Falcariae* (Dittschlag, 1910) and *P. graminis* (Kursanov, 1922) resembles *P. Mariae-Wilsoni* except that in this type the degeneration of the hyphae proceeds so far that there remains only a single layer of potential sexual cells. This cell layer corresponds in appearance to the palisade layer of the caeoma, only it lies inside the hyphal knot instead of on its top. Just as in the palisade cells of the caeoma, these sexual cells occasionally cut off some sterile cells, a thing not yet observed in *P. Mariae Wilsoni*.

In the fourth type, to which, for example, belong *Endophyllum Sempervivi* (Hoffmann, 1912) and *Puccinia Eatoniae* (Fromme, 1914) development is still simpler. Here, on the whole, no special sexual cells are formed, but plasmogamy takes place between any two mycelial cells in the basal region of the plectenchymatic knot, where the fusion cells elongate radially and cut off chains of initial cells as basal cells.

In certain cases, it has been demonstrated that at the base of the aecia plasmogamy rarely takes place; in certain strains of *Endophyllum Euphorbiae-sylvaticae* (Mme. Moreau, 1914), of *E. Centranthi-rubri*

(Poirault, 1913, 1915) and of *Puccinia Pruni-spinosae* (Kursanov, 1914), a layer of palisade cells is normally formed at the base of the aecia. This layer occasionally may cut off a few sterile cells. Although these are still uninucleate, they proceed without apparent cause to differentiate aeciospore mother cells which appear entirely similar to the binucleate ones and, like these, divide into aeciospores and intercalary spores. The aeciospores are naturally uninucleate, *i.e.*, the whole course of development proceeds parthenogenetically. The reverse condition has been demonstrated for another strain of *Endophyllum Euphorbia-silvaticae* (Sapin-Trouffy, 1896; M. and Mme. Moreau, 1918, 1919). In it the whole mycelium is binucleate; consequently plasmogamy at the base of the aecia is omitted and development proceeds apogamously, as will be described later.

The developmental history of the aecidium agrees with that of the caeoma only in so far as plasmogamy generally precedes the formation of the initial cells.

The aecidium is distinguished from the caeoma by its pseudoperidium, which arises as follows: The uppermost aeciospores of a chain occasionally lose their spore character, as is the case in the buffer cells of *Albugo;* they increase in size in all directions, and adhere laterally to similarly deformed spores to form a peridium of a single layer of cells (Fig. 376, 2). As the maturation of the aecidia takes place from the center to the margin, new cells are always added laterally to this cover. When this transformation has reached the periphery, it proceeds basipetally in the outer chains. In these outermost cells, not only the uppermost cells are deformed as peridial cells but the whole of the outermost chains is used for vegetative purposes. The basal cells of these chains proceed with the cutting off the initial cells, thus adding new cells to the pseudoperidium from beneath and enabling it to keep up with the growth of the central spore chains. The pseudoperidium here retains a firm texture as a result of the peculiar development of the intercalary cells. In these outermost chains, therefore, they are not separated directly beneath the aeciospores but obliquely toward the outer side. In this manner, they no longer function as disjunctors and the metamorphosed aeciospores adhere to each other as in the middle of a dome. In most forms, these peripheral intercalary cells degenerate early. In *Puccinia graminis* and *Gymnosporangium juniperinum*, on the other hand, they increase in

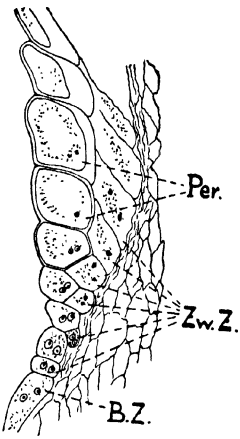


FIG. 377.—*Puccinia graminis*. Peripheral portion of aecidium. Section of the basal cell, *B.z.*, and the lower portion of the peridium, *Per.*, with intercalary cells, *Zw.Z.* (× 500; *after Kursanov*, 1914.)

size as the young peridium and press together to form a layer (Fig. 377) surrounding the pseudoperidium at its base at least and separating it laterally from the plectenchymatic knot (Kursanov, 1914; Fromme, 1914).

The degree of thickening of the peridial cells depends entirely on climatic influences; thus in dry habitats and xerophytic leaf structure, thick-walled peridial cells with narrow lumina are preponderant; in damp habitats and in hygrophil leaf structures, thin-walled cells with broad lumina prevail (Mayus, 1903; Iwanoff, 1907). Moreover, the thickening in each species is characteristic.

At the maturity of the aecidia, the top of the peridium with the host tissue above it is ruptured, the torn edges are bent outwards and thereby create the typical cup form (Fig. 372, 2). In *Gymnosporangium*, they project far over the host tissue and are curiously split into shreds (*Roestelia* type).

The number of aeciospores in a sorus is very large; Fromme (1914) estimates more than 8000 for *Puccinia Eatoniae*, Buller (1924) 11,000 for *Puccinia graminis*. A bush of *Berberis* with 200 infected leaves produces about a billion spores. The aeciospores are very uniform in size, oval or slightly polyhedric, unicellular as the pycnospores but much larger, 15 to 40μ in diameter. Their content is colored orange-yellow, usually by an oily substance. Their membrane is usually thin and colorless, more seldom thick and brown, generally covered with fine or coarse warts or alveoles. They generally contain several germ pores which are usually only visible at germination when the membrane swells up in their vicinity.

The aeciospores, at least in *Gymnosporangium myricatum*, are disseminated by a peculiar elongation, reminiscent of the Entomophthoreae, discharged from the cup (B. O. Dodge, 1924) and then spread mainly by the wind. Immediately after maturity, they are capable of germination; usually they soon lose this power and seldom winter over. Germination occurs usually by a germ tube which penetrates a stoma of the new host and there develops a binucleate mycelium. According to the choice of host plants, two biological types may be distinguished. To one type belong those where the new host is one of the same species as the one which bore the aecium; *e.g.*, in *Phragmidium disciflorum* the uninucleate aecial mycelium develops on *Rosa;* its aeciospores infect other individuals of the same species of *Rosa*. The Uredinales which belong to this type are called **autoecious.** In numerous other species, the germ tubes of the aeciospores show a biologically variable relationship, *e.g.*, in *Cronartium ribicola* the uninucleate mycelium grows on the white pines, among others *Pinus Strobus* and *P. cembra*. The germ tubes of the aeciospores cannot infect *P. Strobus* but only species of *Ribes, e.g., R. nigrum*. The binucleate mycelium which develops from the aeciospores possesses, therefore, other physiological needs and lives on an entirely different

plant usually far removed systematically from the host with the aecial uninucleate mycelium. Uredinales of this type, which for the completion of their life cycle must successively infect two different host species, are called **heteroecious.**

In some genera the method of germination of aeciospores is variable. In *Endophyllum Sempervivi*, they form germ tubes as usual when covered with water; in damp air, they germinate with another form of fructification, as basidia and basidiospores. The basidiospores are again able to infect individuals of *Sempervivum*, while infection by the usual germ tubes has not succeeded. Similarly, the aeciospores of *Gymnoconia Peckiana* (*G. interstitialis*) on *Rubus*, especially late in the season, germinate occasionally with basidia instead of with germ tubes (Kunkel, 1920). Also in *Kunkelia nitens* on *Rubus*, germination normally takes place with basidia and basidiospores; in certain strains of *Gymnoconia Peckiana*, a caeoma of the *Gymnoconia* type (tube germination) and one of *Kunkelia* type (basidiospore germination) appear on the same mycelium; indeed, within the same caeoma both spore types may appear (B. O. Dodge, 1923).

On the binucleate mycelium which arises from the aeciospores germinating with a germ tube, aecia may again arise in some forms, *e.g.*, in the above mentioned species: *Puccinia Senecionis, Uromyces Hedysari-obscuri* and *Phragmidium disciflorum.* The cytological processes which take place in them have been discussed by Kursanov (1916) in *Uromyces Scrophulariae* on *Scrophularia nodosa* and *U. Behenis* on *Silene Cucubalus* (*S. inflata*). After infection by aeciospores had been completed, both uni- and binucleate mycelium was observed in the host plants; the binucleate mycelium has apparently resulted from the uninucleate mycelium by a pseudogamous plasmogamy. Both types of mycelium intermingle; nevertheless the pycnia are formed by uninucleate hyphae. In the hyphal knots one also finds binucleate hyphae, but the basal cells of the pycnospores are entirely uninucleate. The aecia are laid down at the same time as the pycnia. In the primordial knots uninucleate hyphae sometimes predominate, at other times binucleate. The binucleate hyphae proceed apogamously to the direct formation of aeciospore mother cells; between the uninucleate hyphae an isogamous sexual act takes place, and aeciospore mother cells are formed in the normal manner. Somewhat later, at the same point of infection which has already borne pycnia and aecia, a telium is laid down exclusively by binucleate hyphae whose end cells change in a normal manner to the teliospore mother cells.

If one again infects the host with aeciospores formed in the first generation, one obtains a second generation of the fungus normally binucleate but nevertheless forming aecia (and later telia, but never pycnia) in a normal manner. The teliospores are identical with those

formed by the first generation. The aeciospore mother cells arise apogamously, as was already partially the case in the first generation. This production of aecia and telia may be repeated for any number of generations by a new sowing of aeciospores from the present generation. If one uses as the infective material, teliospores which have arisen in any generation, meiosis takes place in the basidia, as we shall see later, and the hyphae which penetrate the host are then uninucleate.

These forms, in which the binucleate mycelium produced by the aeciospores again forms aecia apogamously, are an exception. Generally the binucleate mycelium proceeds to the formation of a third spore form, the urediniospores. As the aeciospores, these are formed in special sori, **uredinia,** either covered by a "peridium" (or buffer tissue) or exposed.

As an example of the covered type, we may cite *Cronartium* (Colley, 1918), *Pucciniastrum* (Ludwig and Rees, 1918; Colley, 1918; Kursanov, 1922; B. O. Dodge, 1923; and Moss, 1926), *Hyalopsora, Uredinopsis, Milesina, Melampsorella* and *Thekopsora* (Moss, 1926). As in the formation of a cacoma, the hyphae intertwine to a flat intramatrical knot (Fig. 378). The upper cells, the spore initials, elongate and cut off a chain of three cells, the upper of which becomes the peridial cell *P*, the middle the disjunctor (not found in *Cronartium*) and the lower, the sporogenous cell which divides into the urediniospore *Sp* and the stalk cell *St*, which may degenerate during maturation of the spores as the intercalary cells of the aecia. Subsequent sporogenous cells are budded out from the basal cell. As in the aecidia, the peridial cells adhere laterally with neighboring cells to form a peridium one cell thick. The disjunctive cell degenerates, freeing the spores from the peridium.

In *Chrysomyxa* (*Melampsoropsis*) the peridium is two cells thick but loose, weakly developed and evanescent, apparently vestigial since the second cell of the chain fails to function as a disjunctor. In *Melampsora*, the peridium consists of an evanscent layer of very thin-walled cells (Kursanov, 1915).

The second type of uredinium, in which the urediniospores arise singly on short stipes without forming a peridium, includes the majority of the known rust genera. An intramatrical hyphal knot is formed here also; each of the hyphal ends at the top of the knot, as the basal cells in the chain type, cuts off an initial cell which divides into a large apical cell, the future spore, and a smaller basal cell, the stipe cell. These, however, do not continue division but grow repeatedly laterally, as do the subterminal cells of *Iola* and *Eocronartium*, and occasionally differentiate at their ends new initial cells which again divide into spores and stipe cells. Therefore the urediniospores lie beside each other in one plane (Fig. 379, 1). These two types, however, are not sharply distinct. Thus in *Melampsorella* both types have been reported.

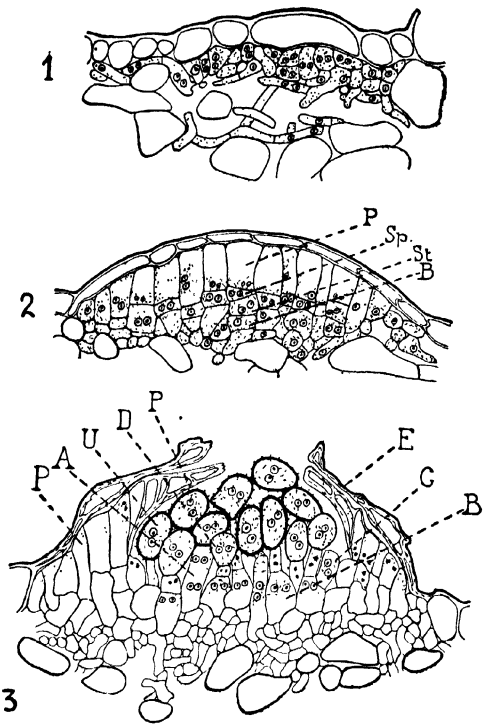


FIG. 378.—*Cronartium ribicola*. Development of uredinium 1. Fundament of sorus and stoma. 2. Older stage. 3. Mature sorus. *P*, peridial cell; *Sp*, young urediniospore; *St*, stalk cell; *B*, basal cell; *A*, multinucleate basal cell before the formation of the urediniospore mother cell, *C*; *D*, spore and stalk cell just formed from urediniospore mother cell; *U*, mature urediniospore; *E*, crushed epidermal cells. ($\times$ 330; *after Colley*, 1918.)

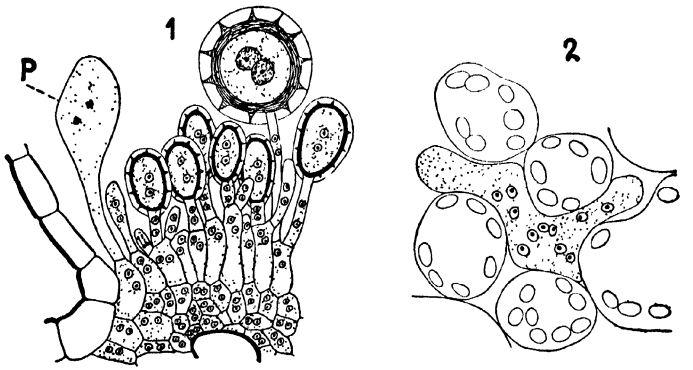


FIG. 379.—*Phragmidium Rubi*. 1. Periphery of uredinium. *P*, paraphyses. *Puccinia glumarum*. 2. Uredinial mycelium in host tissue. (1 $\times$ 565; 2 $\times$ 830; *after Sappin-Trouffy*, 1896, *and Lindfors*, 1924.)

In the structure of the uredinium, there exists as great variety as in the covered type. In some genera, as in *Puccinia*, *Uromyces*, *Phragmidium* and *Triphragmium*, they are surrounded by a margin of peri-physes or intermingled in the interior with paraphyses; and in *Hemileia* the stipes are joined together into a fascicle which emerges from the stoma bearing at its tip a small head of urediniospores. Both types of uredinia have one thing in common, that their spores arise (as the aeciospores) as daughter cells of an initial cell which divides into the future spore and the stipe cell. Thus their development is entirely homologous to that of the aeciospores, but since their mycelium is binucleate after

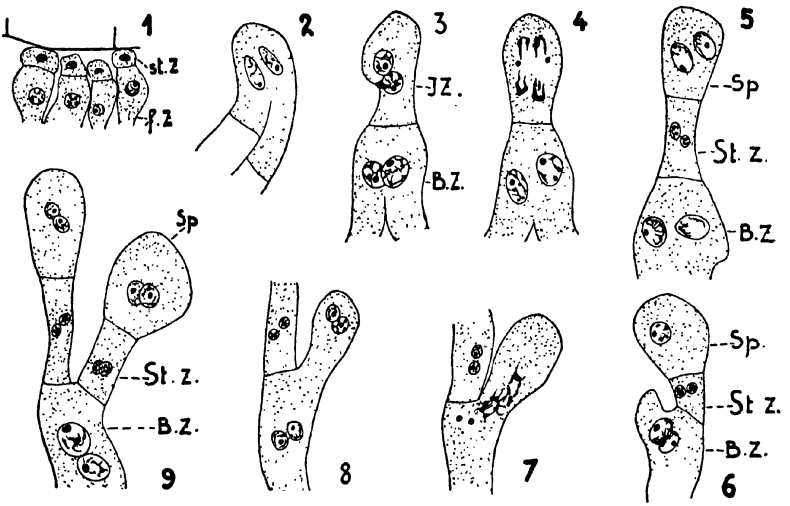


FIG. 380.—*Phragmidium Potentillae-canadensis*. Development of the primary uredinium. 1. Fertile cells, *F.Z.*, have cut off sterile cells, *St.Z.* 2. Fusion. 3. Formation of spore mother cell, *I.Z.*, from basal cell, *B.Z.* 4. First nuclear division in the spore mother cell. 5. The spore mother cell has divided into a spore, *Sp*, and stalk cell, *St.Z.* 6 to 8. Lateral budding of the basal cell to a new spore mother cell. 9. Two mature urediniospores from the same basal cell. (*After Christman*, 1907.)

the aecial stage, there is no plasmogamy before the formation of the initial cells.

Forms in which the aecium closely resembles the uredinium are sometimes said to lack the aecium and the first sorus, except pycnia, is then called the **primary uredinium,** while the later uredinia, resulting from its spores, are called **secondary uredinia.** As far as these forms have been investigated, plasmogamy and further development occurs as in a caeoma (Figs. 380, 381), *e.g.*, in such forms as *Triphragmium Ulmariae* (Christman, 1907; Olive, 1908; Kursanov, 1922; Lindfors, 1924), *Phragmidium Potentillae-canadensis* (Olive, 1908), *Uromyces Alchemillae*, *Puccinia obtegens* (Kursanov, 1922) and probably also in *Kuehneola albida*

(Strelin, 1912). The close agreement which has been found in this respect between the manner of formation of spore and of peridium of the aecidia and uredinia is suggestive. In *Uromyces Glycerrhizae*, plasmogamy appears to occur somewhere on the mycelium, as the hyphae which form the uredinium are already binucleate (Olive, 1913).

These primary uredinia which have arisen on the uninucleate mycelium often differ in their appearance from the secondary ones formed later on the binucleate mycelium, *e.g.*, they are distinguished by a greater size and a consequent greater deformation of the host or by a somewhat different color. Because of the close morphological relationship, it is often impossible to draw a sharp line between aecia and primary uredinia; thus the first sorus of *Phragmidium violaceum* is designated by some authors as an aecium (caeoma) and by others as a primary uredinium.

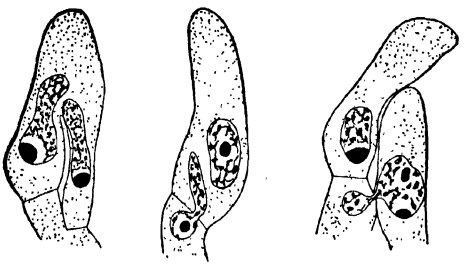


FIG. 381.—*Triphragmium Ulmariae.* Types of cell fusion in the primary uredinium. (× 1,720; *after Lindfors*, 1924.)

The difficulties are in part due to the fact that urediniospores sometimes greatly resemble the aeciospores. They are 15 to 40 μ in diameter, unicellular, ovoid to cuneate, and generally finely echinulate or verrucose, the membrane is generally fairly thick, hyaline to yellow brown, and pierced by several equatorial germ pores which are filled with a substance of variable composition. The number and position of the germ pores furnish important systematic characters. The urediniospores are easily separated from their stipes and are disseminated by winds, as are the aeciospores. Immediately after their maturity they are capable of germination, but lose this ability after a few months. True overwintering of urediniospores is known with certainty in only a few cases, as in *Uredinopsis Struthiopteridis* and *Kuehneola albida*. In continental climates, they may have the opposite task of serving as resting spores during a drought. In all these cases, they possess a very strong brown wall, a persistent stipe and are called **amphispores.**

Germination may take place within very wide limits of temperature, but the ability to infect lies within narrow limits, *i.e.*, in the neighborhood of the optimum for germination. At germination one or more germ tubes penetrate the stomata of the new host and there again develop a

binucleate and, occasionally secondarily, a multinucleate mycelium (Fig. 379, 2). At the germination of the urediniospores there is no change in host. On this binucleate mycelium there may arise uredinia with urediniospores which develop a new mycelium, which again forms uredinia, so that several generations of uredinia with uredinial mycelium follow one another within a single growing period. In the binucleate mycelium, the urediniospores play the same role of rapid propagation as the conidia on the haploid mycelium.

After a definite length of time **telia** (sori of teliospores) appears on the binucleate mycelium. The exact moment of their appearance depends upon the condition of nutrition of the host and generally corresponds with the end of the growing season; it can be retarded or hastened by the environment (Iwanoff, 1907; Morgenthaler, 1910; Gassner, 1916). The teliospores are the homologs of the probasidia and sclerobasidia of the Auriculariales: the dicaryon fuses in them to a single diploid nucleus which gradually prepares for meiosis. In contrast to the urediniospores, which arise during the diplophase, the teliospores terminate this diplophase.

In addition to these normal forms, in which the telia arise on the binucleate mycelium, telia (in forms which lack the aecia and uredinia) may be formed directly on the uninucleate mycelium. In this respect five groups may be distinguished. In the first group, to which belong *Uromyces scutellatus*, *U. laevis*, *Puccinia Fergussoni*, *P. Rossiana*, *Chrysomyxa Abietis* (Kursanov, 1922), *Uromyces alpestris* (Tranzschel, 1910) and *Gallowaya pinicola* (B. O. Dodge, 1925), the telia closely resemble the aecia; thus in *U. alpestris* they are formed in the interior of aecidia which do not open as such, and in *U. scutellatus* on *Euphorbia* the remains of the aecidial fundaments are indicated by peridial cells in the young telia. In their development, they correspond to aecia, *e.g.*, those of the type of *Puccinia Violae:* the thick hyphal knot is differentiated into an upper sterile and lower fertile zone. Between two palisade cells or between two vegetative cells or between a palisade cell and a vegetative cell, plasmogamy occurs and the fusion cells develop to short, branched hyphae on whose ends are formed the teliospores. Similarly, the telia of *Puccina Anemones* (*P. fusca*) on *Anemone nemorosa* develop exactly as the aecia of *Ochropsora Ariae* on the same host (Lindfors, 1924).

In a second group including, among others, *Puccinia Malvacearum* (Mme. Moreau, 1914; Werth and Ludwigs, 1912), *P. transformans* (Olive, 1908), *P. Buxi* (Mme. Moreau, 1914) and probably also *P. Liliacearum* (Maire, 1899), differentiation occurs as in a caeoma: on the top of the hyphal knot there are formed palisade cells which copulate with each other or with hyphal cells.

In a third group, *e.g.*, *Uromyces Ficariae* (in which the uredinium is acking) there is, as in *Endophyllum Sempervivi*, no definite palisade forma-

tion and plasmogamy takes place, as may occasionally happen in *Puccinia malvacearum* (Lindfors, 1924), at the base of the hyphal knot between two neighboring hyphal cells (Mme. Moreau, 1914) or even before the formation of the telia, between two ordinary mycelial cells (Blackman and Fraser, 1906).

In a fourth group, *e.g.*, *Uromyces Scillarum* (Blackman and Fraser, 1906; Mme. Moreau, 1914), *Puccinia Adoxae* (Blackman and Fraser, 1906) and *P. Aegopodii* (Kursanov, 1922), plasmogamy takes place between two vegetative cells long before the formation of the telia.

In the fifth group, finally, to which belongs *Uromyces Rudbeckiae* (Olive, 1911), plasmogamy is entirely lacking and the life cycle is apomictic in the uninucleate phase, as in *Endophyllum Euphorbiae-silvaticae* and some strains of *Caeoma nitens*.

As teliospores of all five forms of fructification in the Uredinales have undergone very great differentiation in form and appearance, they offer very important characters for systematic groupings within the order. In them are four types which correspond to the families: Coleosporiaceae, Melampsoraceae, Cronartiaceae and Pucciniaceae.

Coleosporiaceae.—In the Javan *Goplana mirabilis* on leaves of *Meliosma*, the sorus is extramatrical on the underside of the leaf, where it

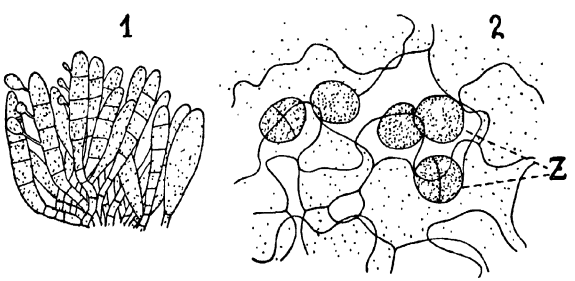


FIG. 382.—1. *Goplana mirabilis*. Hymenium. 2. *Uredinopsis filicina*. Zeugite, *z*, in spongy mesophyll. (1 × 320; 2 × 410; *after Sydow*, 1915, and *E. Fischer*, 1904.)

looks macroscopically like a simple species of *Septobasidium*. The terminal cells of the extramatrical mycelium change as in the latter to a basidium; the subterminal cells develop laterally, as in *Iola*, to new basidia so that finally every hypha bears a small cluster of basidia (Fig. 382, 1). The peripheral cells of the sorus remain sterile and are transformed into periphyses.

In *Coleosporium Sonchi-arvensis* (Sapin-Trouffy, 1896), *C. Solidaginis* (Holden and Harper 1902) and *C. Campanulae* (Juel, 1898), the binucleate, intercellular hyphae grow out of the interior of the host tissue toward the epidermis and come together beneath it to form a palisade layer (Fig. 383, 1). The terminal cell of each hypha

swells greatly and the dicaryon fuses, forming a single diploid nucleus. The zeugites elongate, forming the basidia. Because of the mutual pressure under the epidermis, they are flattened next each other and form a compact layer which is imbedded in a gel secreted by the membranes. In some species the basidia are thickened at the tip. This is primarily a biological adaptation, since the tips must rupture the epidermis by their pressure. After a time the basidia divide, as in *Auricularia*, into

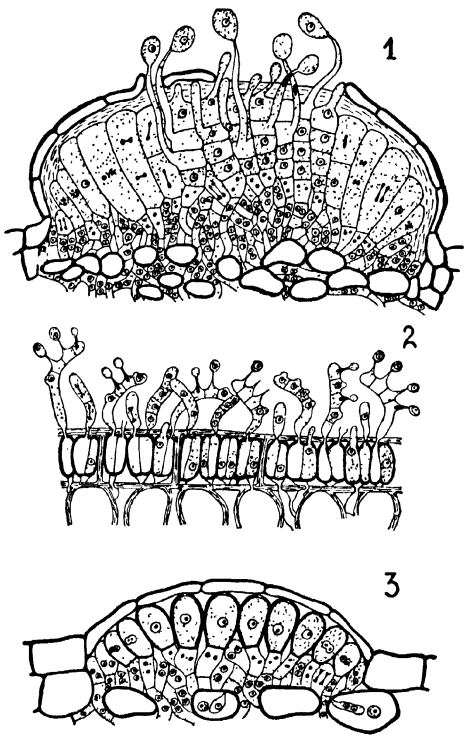


FIG. 383.—1. *Coleosporium Sonchi-arvensis*. Hymenium. 2. *Thekopsora areolata*. Telium. 3. *Melampsora Helioscopiae*. Telium. (1 × 270; 2, 3 × 340; *after Sappin-Trouffy*, 1896.)

four cells, each cutting off a basidiospore and raising it above the ruptured epidermis on a long sterigma.

In *Gallowaya pinicola* (B. O. Dodge, 1925) there is very little intertwining of hyphae as a preliminary to the formation of the telial sorus. The hyphae grow out through the mesophyll and form a palisade of chains of four or five uninucleated cells. The terminal cells form the peridium as in the covered type of aecidium or primary covered uredinium. Soon after the epidermis is ruptured cell fusions occur between

the second or third cells from the outer ends of the chains, the separating walls completely disappearing. At the same time the buffer cells above collapse, like the disjunctive cells in the uredinium. The fusion cell divides immediately, the upper cell taking most of the cytoplasm, leaving the lower cell vacuolate. This upper cell then forms a short chain of binucleate cells which occupy the space below the peridium. Caryogamy begins in the terminal cell of these chains and proceeds slowly basipetally. The now uninucleate zeugite elongates and forms the typical four-celled basidium of the *Auricularia* type. After the basidiospores have been shed, the basidium collapses and the cell below elongates and forms a basidium. This process may continue until all the binucleate cells are used up, but age of the sorus and mechanical difficulties in raising the lower basidia high enough to secure complete dissemination of basidiospores, usually results in the failure of the lowest cells to function properly.

Here we have the diploid phase and the binucleate mycelium reduced to its lowest possible amount, without even the differentiation of teliospores as such, consequently this species in some ways seems more primitive than *Septobasidium* and might be placed in *Auricularia*, except for the catenulate basidia. Similarly the so-called teliospores of *Coleosporium* are rather to be regarded as thick-walled basidia. The sorus consists exclusively of fertile basidia, while in *Auricularia* there are sterile paraphyses. Similarly the sorus should be regarded as basidial hymenium, not telium. In order not to confuse their terminology, however, systematists have used teliospore for structures which appear in the same position as true teliospores do in other rusts. These "teliospores" germinate "internally," directly to basidia. From the standpoint of comparative morphology, it must be emphasized that the Coleosporiaceae lack teliospores.

Melampsoraceae.—As the Coleosporiaceae correspond to the Auriculariaceae, this family exhibits the developmental tendency of the Septobasidiaceae. The zeugites increase in independence and become special storage organs in which the nutrients are prepared for the moment most favorable to basidial formation. The basidia agree extensively in their habits with *Septobasidium*, and are without stipes, lateral or terminal on hyphae; only they are formed (as is the character of the rusts) endoparasitically, exclusively within the host instead of upon its surface.

In *Uredinopsis* (Faull, 1928), the teliospores arise in scattered groups just below the epidermis, occasionally a few in the mesophyll. They have a thin, hyaline, smooth membrane and are spherical or elongate, septate and capable of germination early the following spring (Fig. 382, 2).

In *Melampsorella*, they are similar but are formed within the epidermal cells and, in case several are laid down in the same cell and the space is not sufficient, they are flattened sidewise. They develop on new leaves

in the spring and germinate immediately with an apical basidium which ruptures the wall of the host cell and produces its spores outside the epidermis. In *Milesina* they develop on overwintered fronds and germinate at once.

While in *Melampsorella* and *Milesina* the zeugites, because they are not encysted, should not be designated as teliospores in the true sense of the word, in *Thekopsora*, *Pucciniastrum* and *Melampsora* they have a firm membrane and become hypnospores. Besides, they do not arise individually scattered over the host tissue but are collected in more definite sori as true telia. In *Thekopsora*, they occur in the epidermal cells, usually several in one cell, almost completely filling it and by mutual pressure adhering in a plate (Fig. 383, 2). They divide by vertical or somewhat oblique walls into two to four daughter cells, each of which sends out a basidium. *Pucciniastrum* behaves similarly, its telia instead of being intracellular are intercellular under the epidermis. In *Melampsora* (Fig. 383, 3) the teliospores are joined laterally into a hypodermal or subcuticular crust; in them, however, the longitudinal division into daughter cells is absent.

Faull (1928) summarizes developmental tendencies within the family as follows: *Uredinopsis*, *Milesina* and *Hyalopsora* are restricted to *Abies* and ferns, while the others are found on *Abies*, *Larix* or *Picea* and angiosperms, although in the latter case none are known on recent families such as Orchidaceae and Compositae. The characteristic yellow pigment of rusts is lacking in *Uredinopsis* and *Milesina*, being present in the other genera. The pycnia are comparatively large and deep seated in *Uredinopsis*, *Milesina* and *Hyalopsora* and small and superficial in the others, becoming quite abortive in *Calyptospora*. The uredinium is quite constant but absent in *Calyptospora*. It is the largest in *Uredinopsis*, its peridium being simple in *Uredinopsis*, *Milesina*, *Hyalopsora* and *Melampsorella* and showing specialization in *Pucciniastrum*, *Thekopsora* and *Melampsoridium*. The telia are diffuse especially in *Uredinopsis*, less so in *Milesina*, *Hyalopsora* and *Melampsorella*, tending to become compact in *Pucciniastrum*, *Thecopsora*, *Melampsoridium* and *Calyptospora*. They are subepidermal in *Uredinopsis*, *Pucciniastrum* and *Melampsoridium*, intraepidermal in the other genera; they are occasionally subepidermal in *Milesina*. The teliospores are irregular in form and number in *Milesina* and *Hyalopsora*.

Cronartiaceae.—Here the teliospores are morphologically at approximately the same stage of development as the Melampsoraceae. Several spores are cut off catenulately on the hypha, and the whole spore mass of the sorus clings together into a columnar spore body. In *Cronartium ribicola* the telia so extensively agree with the earlier described uredinia in the young stages, *e.g.*, in the formation of the hyphal knot, peridium and sporiferous basal cells, that in this stage it is not possible to dis-

tinguish them. The initial cells change entirely into teliospores instead of dividing into spores and intercalary cells. They remain connected with one another and, by the increase of new cells on the lower side, form a lengthening column which finally ruptures the peridium and passes out through the epidermis (Fig. 384, 1). The teliospores are thin-walled, apically thickened and capable of immediate germination at maturity (Fig. 384, 2 to 7).

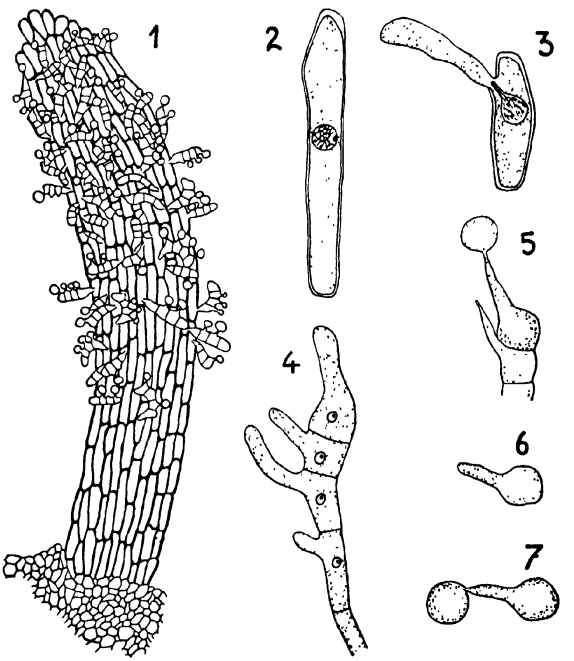


FIG. 384.—*Cronartium ribicola*. Short column of teliospores with teliospores already germinated in the upper portion. 2. Mature teliospore. 3. Beginning of germination. 4. Basidium. 5. Tip of basidium with basidiospore. 6, 7. Germination of basidispores. (1 × 115; 2 to 7 × 565; *after Colley*, 1918.)

The telia of *Chrysomyxa* (Fig. 385) are similar in their structure but lack the peridium; in *Chrysomyxa Abietis*, however, the development of the teliospores is somewhat more complicated. Each of the fusion cells, which here, as in *Uromyces scutellatus* and *Gallowaya pinicola*, result from the fusion of two palisade cells, elongates much and divides into an apical "sporoid cell," which subsequently swells and thickens its wall, and into a basal cell, which remains slender and thin walled. The sporoid cell may divide by septa into two or three chambers and winter over in this condition. In spring each chamber forms a projection, into which

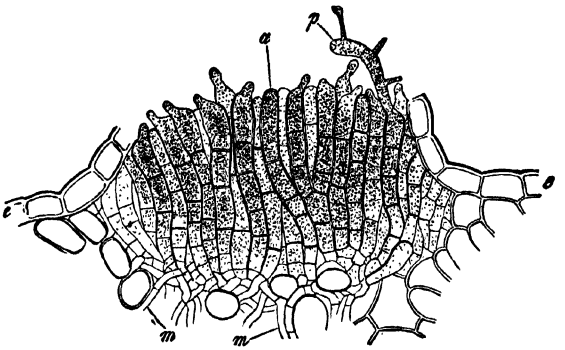


FIG. 385.—*Chrysomyxa Rhododendri.* Telium. *a*, catenulate teliospores (zeugites); *p*, basidium; *e*, epidermis of host; *m*, mycelium. (*After Bary*, 1884.)

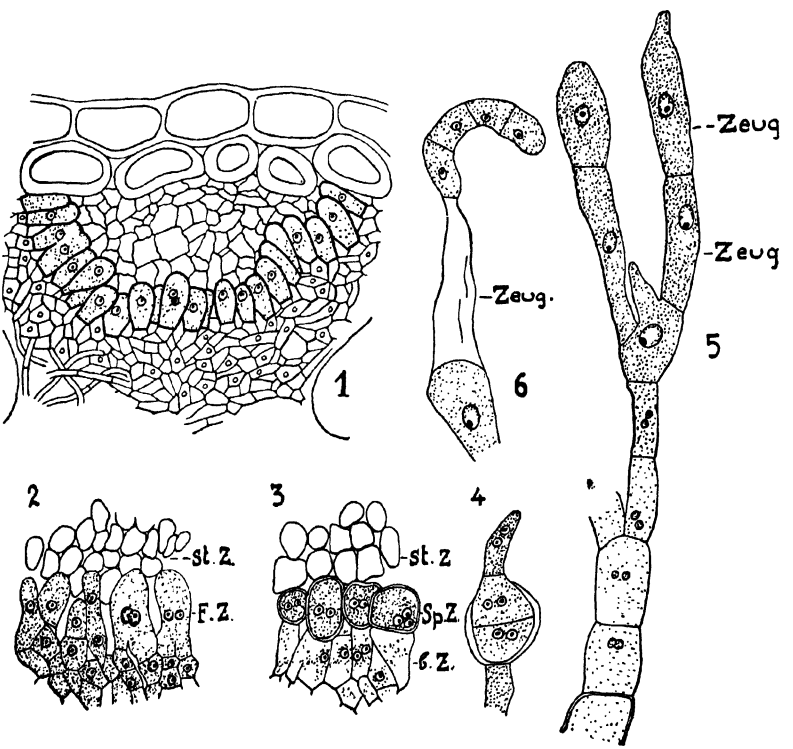


FIG. 386.—*Chrysomyxa Abietis.* Development of telium. 1. Older sorus with sporoid cells. 2. Copulation of fertile cells. *F.Z.*, fusion cell; *St.Z.*, sterile cell. 3. Fusion cell has divided into sporoid cell, *Sp.Z.*, and basal stalk cell, *b.Z.* 4, 5. Germination of sporoid cells to a chain of zeugites. 6. Germination of zeugite. (1 to 4 × 500; 5, 6 × 600; *after Kursanov*, 1922, *and Lindfors*, 1924.)

a dicaryon migrates, occasionally branches and cuts off at the ends a series of thin-walled teliospores which are at once capable of germination. Furthermore in floras two other genera are included, *Endophyllum* and *Kunkelia*, whose aeciospores, as mentioned earlier, occasionally germinate with a basidium, as do teliospores. As the descriptive systematist, on practical grounds, regards the germination of the spores as decisive, he designates these structures as teliospores, while the comparative morphologist must consider them as aeciospores because of their ontogeny.

Pucciniaceae.—Here appears an entirely new phenomenon: the teliospores are stipitate as the urediniospores, and they arise as daughter cells of one mother cell which divides into the teliospore and the stipe cell. The binucleate hyphae push forward from the interior of the host toward a definite point of the epidermis, join together to a loose stroma, swell terminally and change their end cell to a basal cell. Only in *Gymnosporangium*, the subterminal cells function as basal cells and the terminal cells degenerate and become buffer cells (B. O. Dodge, 1918, 1922). By lateral growth the basal cells are able to repeat the formation of initial cells, just as in the uredinia (Fig. 388, 5). At maturity, the epidermis is ruptured by the pressure of the whole telium and individual spores lie free. In contrast to the urediniospores, they usually remain closely adherent to their stipes and germinate *in situ*. Before germination, the dicaryon fuses to a diploid nucleus: the teliospores here play the role of zeugites.

In the simplest cases, as in the Asiatic *Blastospora*, in the West Indian *Botryorhiza* and in the cosmopolitan heterogeneous *Uromyces*, they consist of a single cell whose wall, in *Blastospora* (Fig. 389, 1) and *Botryorhiza* (Fig. 387, 1), is hyaline and thin, and in *Uromyces* (Fig. 387, 2) is usually brown and thick, bearing a curious, apical, germ pore. In *Blastospora*, they germinate without a rest period; in *Uromyces*, they are generally true resting spores.

In the following genera, the apical daughter cell destined for a spore, before the thickening of its wall and the fusion of the dicaryon divides by septa into two or more chambers each of which, at germination, produces a basidium.

In *Puccinia* (Fig. 387, 3) there are two chambers, of which the upper possesses an apical germ pore, the lower a lateral one. In certain species, however, the formation of the septum may be entirely absent, so that many spores, in some cases even a majority, in the telium remain unicellular. As, however, the two-celled spore form is considered the higher for purposes of classification, the species must be placed in *Puccinia;* and then the spores which have remained unicellular are called **mesospores.** In certain other species, there are at times produced two habitually different spore forms; thus *Puccinia Veronicarum*, in spring and summer,

forms a naked, dusty telium whose spores are mostly thin walled and colorless, clinging to the stipe and germinating directly (forma *persistens*). In the fall is formed a compact cushion in which the fungus winters over

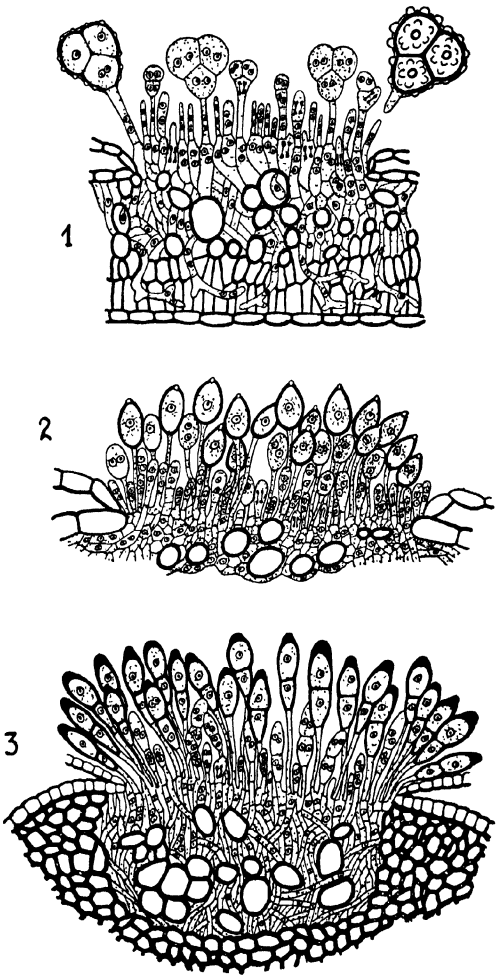


FIG. 387.—1. *Botryorhiza Hippocrateae*, section of mature and young telium. 2. *Uromyces striatus*; 3. *Puccinia graminis*. (1 × 330; 2, 3 × 300; 1 *after Olive*, 1918; 2, 3, *after Sappin-Trouffy*, 1896.)

and whose spores, thick walled and yellow brown, falling easily from the stipe, can germinate only after a winter's rest (forma *fragilipes*).

In *Gymnosporangium* the number of daughter cells is generally two; in *Phragmidium* (Fig. 388, 1 to 4), it may reach twelve. In both genera,

the membrane of the spore stipe changes into a substance capable of swelling in damp weather, leading, especially in *Gymnosporangium*, to a gelatinization of the telium. The mature spores are capable of immediate germination, and in *Gymnosporangium* are thin walled in the interior of the sorus.

In *Gymnoconia*, *Triphragmium* and *Kuehneola*, the teliospores have developed in a special direction. In *Gymnoconia* (Fig. 389, 4 and 5) the apical cell divides, as in *Puccinia*, into two superimposed daughter cells. Their germ pores are much distended and their form very variable. In *Triphragmium* (Fig. 390) they divide triangularly into three daughter

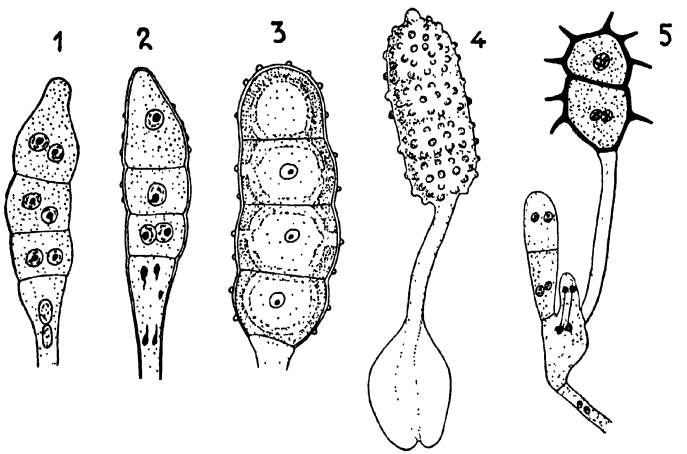


FIG. 388.—*Phragmidium violaceum*. 1. Young teliospore with stalk. 2. Somewhat older stage. 3. Section of mature teliospore showing germ pores. 4. Teliospore with swollen base. 5. *Puccinia Podophylli*. Development of teliospore. (1, 2 × 700; 3 × 535; 4 × 300; 5, partly diagrammatic; *after Blackman*, 1904; *Christman*, 1907.)

cells, the lowest sessile on the stipe. In *Kuehneola* (Fig. 389, 8) they cut off successively, single unicellular teliospores which lie one above the other in a chain, as the chambers of *Phragmidium*, except that they arise in basipetal sequence instead of by repeated division into two, and are consequently not surrounded by a common membrane of the mother cell. The teliospores of *Gymnoconia* and *Triphragmium* are true resting spores, those of *Kuehneola* are capable of immediate germination at maturity.

The following genera are connected directly to *Uromyces* in the form of their teliospores which do not arise in hypodermal telia but are associated in special spore masses raised above the host tissue.

In one direction has developed *Hemileia* (Fig. 391, 2), whose teliospores, like the urediniospores which belong to it, are cut off at the tip from a columnar fascicle of hyphae and are bound together by a gelatinous sheath into a spore head which falls apart by pressure.

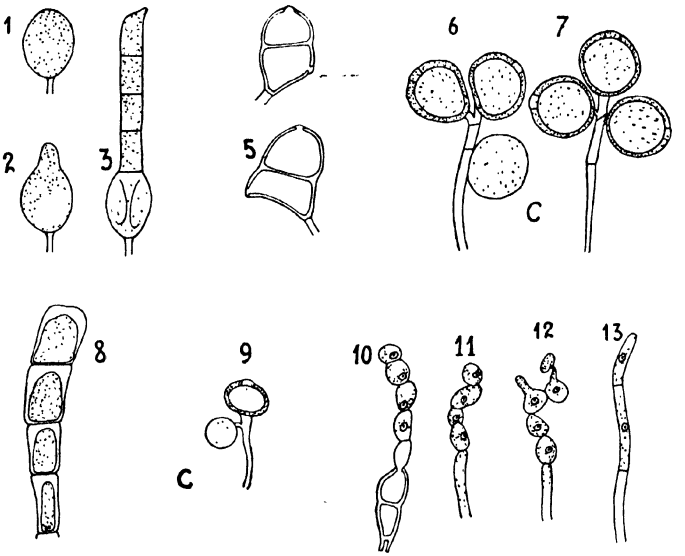


FIG. 389.—*Blastospora Smilacis.* 1 to 3. Germination of teliospores. *Gymnoconia Peckiana.* 4, 5. Mature teliospores. *Uromycladium maritimum.* 6, 7. Teliospores. *C*, cyst. *Kuehneola albida.* 8. Chain of teliospores. *Uromycladium simplex.* 9. Teliospores. *Puccinia malvacearum.* 10 to 13. Germination of teliospores. (1 to 3 × 270; 4 to 9 × 320; 10 to 13 × 230; *after Dietel*, 1908; *Sydow*, 1915; *McAlpine*, 1906; *Klebahn*, 1914; *and Sappin-Trouffy*, 1896.)

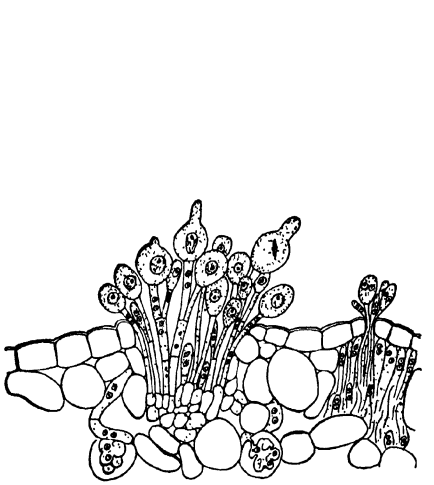


FIG. 390.

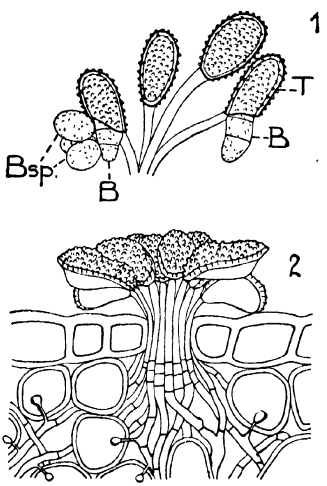


FIG. 391.

FIG. 390.—Telia of *Triphragmium Ulmariae.* (× 300; *after Sappin-Trouffy*, 1896.)

FIG. 391.—*Zaghouania Phillyreae.* 1. *T*, teliospore; *B*, basidium; *Bsp*, basidiospore. 2. *Hemileia vastatrix.* Group of teliospores. (× 320; *after Patouillard from Hariot*, 1908, *and Sydow*, 1915.)

In another direction, *Uromycladium* and *Ravenelia* have been differentiated. In the simpler forms, as *Uromycladium simplex* (McAlpine, 1905), there arises at each terminal cell a teliospore deceptively similar in form and structure to *Uromyces* (Fig. 389, 9). The basal cell changes into a double-walled, hyaline cyst *c* filled with a gel capable of swelling (a characteristic of both genera). Exceptionally, the cysts may be absent and replaced by a second teliospore. In other forms, *e.g.*, *U. bisporum*,

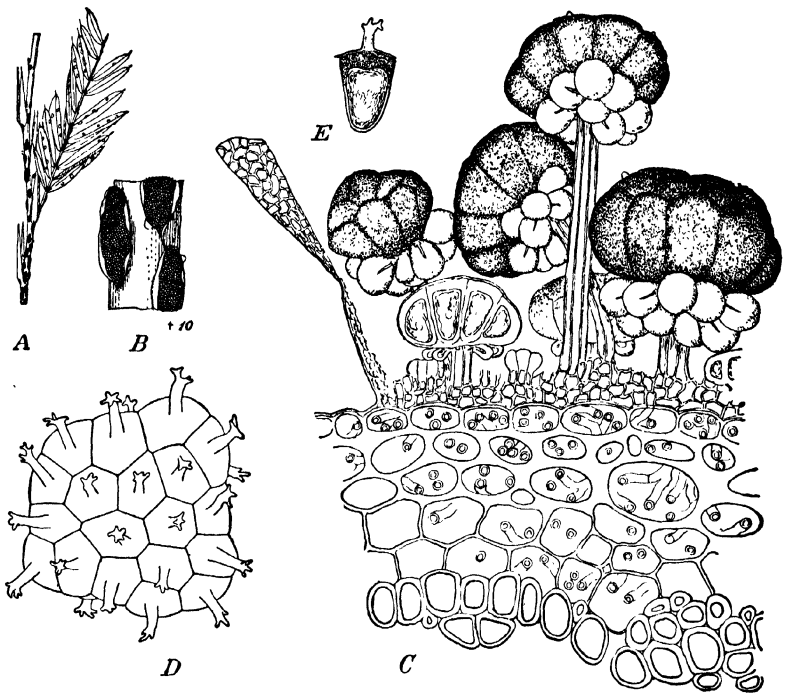


FIG. 392.—*Ravenelia cassiaecola*. *A*. Infected twig of *Cassia nictitans*, with telium on stem and uredinium on leaf. *B*. Enlarged section of stem. *C*. Section through periphery of telium on stem. The cuticle is ruptured. Mycelium visible in the cells of the bark. Telium shows mature and young heads, one in cross section. *Ravenelia appendiculata*. *D*. Head seen from above. *E*. Isolated spore. (*A*, natural size; *B* × 10; *C* × 350; *D*, *E* × 400; *after Dietel*, 1906.)

the sporiferous hyphae regularly produce two teliospores without cysts. Still others, as *U. maritimum*, develop two teliospores (Fig. 389, 6 and 7) above a third cell from which a cyst is developed; here also, in an exceptional case, the cyst may be replaced by a third teliospore. And finally in the highest forms, *e.g.*, *U. Tepperianum*, three teliospores without cysts are regularly formed on the stipe cells.

In *Ravenelia* (Fig. 392), a very significant development of spore heads appears (Parker, 1887; Dietel, 1906). The first fundament of the heads

consists of a fascicle of hyaline hyphae whose ends are rich in plasma and clavately swollen. Every cell divides by a septum into an apical and a basal cell which latter undergoes no further division, but elongates and becomes the stipe cell. The apical cell, under certain conditions, is divided by a longitudinal wall into daughter cells whose number is characteristic for each species. This apical cell divides into an upper spore cell and a lower cyst cell. The spores adhere laterally in a firm dome. In this type, there arise as the spore bodies a definite number of spores and cysts, constant for each species, which are also borne by a definite number of hyphae. In other groups, the relationships are more complicated in that the peripheral spore cells differentiate as cysts; in the central ones septation is absent whereas, in still others, the spores themselves become septate and two celled. The cysts in this genus are filled with a viscid substance and burst at maturity. Their function is not yet clear; possibly they serve for water storage or they facilitate the separation of spores from the sporiferous hyphae or attach the spores to a new substrate.

In contrast to all these forms, which have probably evolved from *Uromyces* in an ascending series, there are three other genera which are best considered as a degradation series. In *Zaghouania* (Fig. 391, 1) and *Cystopsora*, the basidia do not reach the open air through a germ pore from the teliospore but are completely formed within it, rupture the teliospore wall near the stipe and only protrude their tip from the slit; perhaps we have here an adaptation to a dry climate. *Ochropsora* no longer forms teliospores and the basidia arise directly from binucleate mycelium, as in *Coleosporium*. Since transitional forms are still unknown, the significance of these three genera is naturally ambiguous.

The germination of teliospores, as that of the probasidia of the Auriculariaceae, produces a new spore form with basidia and basidiospores. The single cells form a short germ tube through the germ pore, into which the diploid nucleus migrates. That its first division is meiotic has been definitely proved for *Cronartium ribicola* among others, since in the first stage of division sixteen chromosomes have been counted, while the haploid chromosome number is eight (Colley, 1918). The basidia are regularly pleurosporous phragmobasidia, as those of the Auriculariaceae, but there are exceptions, such as *Coleosporium Pulsatillae* where the septa are vertical as in the Tremellaceae (Weir, 1912). All the sterigmata are equally short in the simpler forms, as in the Coleosporiaceae (or in *Auricularia* and *Iola javensis* of the Auriculariaceae). When mature they excrete at their tip a small drop (9 to 10μ) which pushes the basidiospore to one side. When the basidiospore and drop are suddenly hurled away, with the aid of air currents, they are thrown nearly a millimeter; an initial velocity of about 9 cm. per second is reached (Dietel, 1912; Buller, 1924).

Under unfavorable conditions, as under water or in too low oxygen pressure, the germ tube of many species, as *Puccinia Malvacearum* (Klebahn, 1914) and *P. graminis* (Jaczewski, 1910), as also the aeciospores with basidial germination as in *Endophyllum Sempervivi* (Nypels, 1897), develops to long, slender, branched hyphae which form basidiospores only when they reach the surface. In still other forms, as *Gymnosporangium clavariaeforme* (Blackman, 1904) and occasionally also *Puccinia Malvacearum* (Fig. 389, 10 to 13), the four basidial cells round up and fall apart at the least shock; they germinate, according to the environment, with a germ tube or a conidium (basidiospore). Whether these

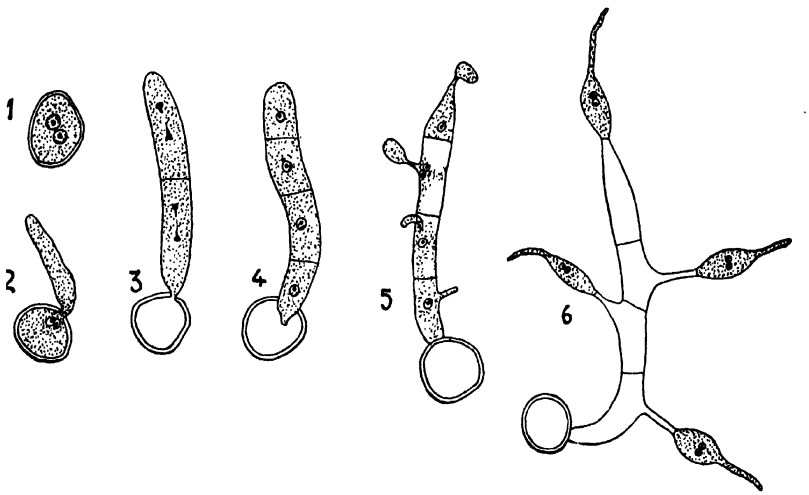


FIG. 393.—*Endophyllum Euphorbiae-silvaticae.* Germination of apogamous aeciospores. (× 665; *after Moreau*, 1919.)

phenomena are abnormalities or have a biological meaning, is still questionable.

In *Puccinia Helianthi*, the mycelia from germinating basidiospores are heterothallic. If they fail to anastomose with other mycelia of the opposite sex, they produce only pycnia, while if a union of + and − mycelia occurs, aecia are produced. Occasionally small aecia of uninucleate aeciospores are produced by the mycelium from a single spore (Craigie, 1927).

In the apogamous forms (p. 569), *e.g.*, *Endophyllum Euphorbiae-silvaticae* (Moreau, 1919), the two nuclei of the aeciospore migrate into the basidium, behave there as the two daughter nuclei of the primary basidial nucleus, become separated by a septum (Fig. 393, 3) and develop normally. The binucleate condition appears again, as in normal development, at the base of the aecium or as a result of previous nuclear division

in the basidium and the basidiospores again become binucleate (Fig. 393, 6). Similarly, it is assumed that in *Puccinia Podophylli* the teliospore-forming apogamous aecia may arise on the perennial binucleate mycelium (Olive, 1913). In *Endophyllum Valerianae-tuberosae* (Maire, 1900), in which caryogamy is sometimes absent, one nucleus in the aeciospore degenerates, leaving the basidiospore uninucleate.

Since we have discussed individually each of the five spore forms of the rusts, we will now consider the form and manner in which the life cycles of the different species are related. As representative of the type in which all forms appear, may be cited the beet rust, *Uromyces Betae*. In it there appear in spring from the basidiospores, uninucleate mycelia which form pycnia with pycnospores and aecia with aeciospores. At the base of the aecial chains, plasmogamy occurs. The aeciospores are dispersed to other beet leaves, are capable of immediate germination and develop to new binucleate mycelia on which appear uredinia and urediniospores, able to germinate immediately and to infect new leaves, where again they may form binucleate mycelia on which uredinia appear. Toward autumn, telia with teliospores arise on all these binucleate mycelia. Caryogamy occurs in the teliospores which winter on the fallen leaves and in the spring germinate meiotically with basidia and basidiospores. The basidiospores again reach young beet leaves and develop there to uninucleate mycelia.

The life cycle which takes place in the limits of a growing period, at least under European conditions, may be expressed in the following scheme:

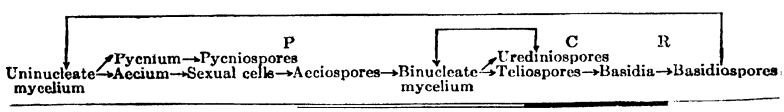


DIAGRAM XXXIII.

In this diagram it is noteworthy that haplont and diplont, as in *Olpidium*, possess individual thalli. In the life cycle of *Uromyces Betae* an alternation of generations proceeds with change of nuclear phase. The gametophyte consists of the uninucleate mycelium which arises from basidiospores and forms pycnia and aecia. The sporophyte consists of binucleate mycelium arising from aeciospores and forming first urediniospores and then teliospores. As both gametophyte and sporophyte in *Uromyces Betae* live on the same host, this alternation of generations can only be discerned cytologically. In the heteroecious forms, it coincides with alternation of hosts; thus, as has been shown above, *Cronartium* thrives in the haploid portion on *Pinus* and in the diploid portion on *Ribes*. Gametophyte and sporophyte here differ physiologically and are specialized on hosts systematically far apart.

Furthermore, it is noteworthy that normally not an aecial but a uredinial mycelium arises from aeciospores. Similarly from teliospores, only basidia and later aecia may be formed. The gametophyte, therefore, consists only of a short generation, that from the basidiospore to the aecium, *i.e.*, it is unable to propagate itself. The only haploid fructifications which arise on the haploid mycelium, pycnospores, are generally not functional. In the heteroecious forms, therefore, the change of host of the gametophyte is obligatory; the gametophyte can only develop further if the aeciospores are able to reach the alternating host. It is different with the sporophytes. Here binucleate mycelium with urediniospores may always arise from the urediniospores as long as climatic conditions or the development of the host plant allows, so that an indefinite number of generations of uredinial mycelium and urediniospores follow one another. As the urediniospores, at germination, always infect the individuals of the same species of host as that on which they have arisen, the sporophyte is able to multiply indefinitely (as in *Olpidium Viciae*, by the zoosporangia). Consequently in the heteroecious species, the change of host is only facultative; only if the sporophyte is forced by environment to form teliospores is it obligatory to change host, as the basidiospores can only infect individuals of the gametophytic host. From the point of view of change of nuclear phase, this innate unlimited repetition leads to an increased duration of the sporophyte which subsequently predominates over the gametophyte.

Forms which correspond to this scheme of development, in which the gametophyte forms pycnia and aecia and the sporophyte uredinio-, telio- and basidiospores, are called "eu-" forms (with complete life cycles) as *Eu-puccinia* or *Eu-uromyces*. In systematic literature, these spore forms are indicated by the symbols 0, I, II, III, where 0 indicates pycnia which are often facultative in appearance, I aecia, II uredinia and III telia. The basidia are not specially mentioned in this case as they always appear at the germination of the teliospore. Of the cytologically investigated forms, *Cronartium ribicola*, *Puccinia graminis*, *Phragmidium violaceum* and *Puccinia Violae* belong to this type.

Besides these Eu-forms, a great number of species are known in which one or another of the spore forms is absent and the life cycle is "incomplete." These other types of cycle are given special names: the four most important, -opsis, endo-, brachy- and micro- types, will be discussed here.

In the -opsis forms, *e.g.*, in *Gymnosporangium* and in *Puccinia Falcariae*, the urediniospores are lacking, in other species the pycnia also. The life cycle corresponds entirely with that of the eu- forms, only the expansion of the sporophyte, because of the repetition of urediniospores, is absent. In some earlier mentioned species, as *Puccinia Senecionis* and *Uromyces Hedysari-obscuri*, this gap is filled by the apogamous repetition

of aecial formation. The eu- and -opsis forms are called long-cycled forms, the other (endo-, brachy- and micro- forms) are called short-cycled forms. In the endo- type (0, I) both urediniospores and teliospores are lacking, *e.g.*, *Endophyllum Sempervivi* on *Sempervivum*. The uninucleate mycelium penetrates the whole leaf parenchyma and winters over in the host. It first forms pycnia, then aecia. Plasmogamy occurs in the aecia, as was earlier shown, with consequent dicaryons which fuse in the aeciospores. These germinate (normally) with basidia whose spores again infect *Sempervivum* leaves. In the endo- type accordingly, the aeciospores have taken over, caryologically and biologically, the function of teliospores. The life cycle may be indicated as follows:

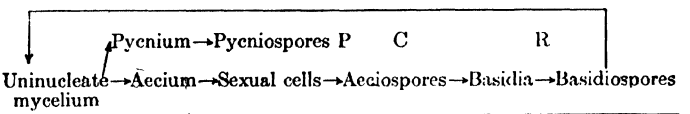


DIAGRAM XXXIV.

The gametophyte is formed as in the eu- forms, while the sporophyte has lost its individuality: it is limited to the aeciospores, on whose germination meiosis takes place. Its height of development places it at the same stage as the diplonts of the Phycomycetes.

In contrast to the endo- forms, the brachy- and micro- forms are distinguished by the lack of aecia, the micro- forms by the further lack of uredinia. As far as the brachy- forms (0, II, III) have been investigated, a typical sexual act occurs in the uredinium which takes the place of the aecium in the life cycle. In *Triphragmium Ulmariae* the basidiospores germinate to a uninucleate mycelium. On this are formed pycnia and large primary uredinia of irregular shape. In the latter, sexual acts occur, the spores of the primary uredinium again infect plants of *Ulmaria* and develop there to binucleate mycelia which form small, rounded, secondary uredinia and later telia. Its life cycle proceeds according to the following scheme:

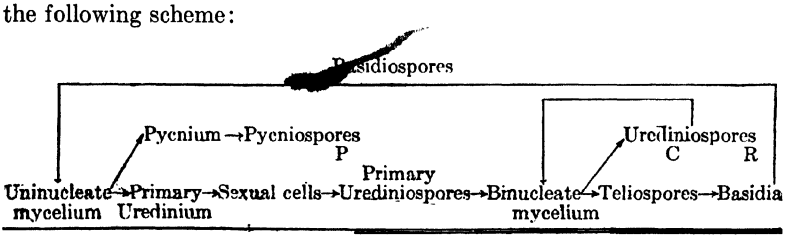


DIAGRAM XXXV.

It is essentially correct even to pycnia, often absent as in the eu-forms, but the primary uredinia are substituted for aecia.

In the micro- type (0, III), finally, the life cycle becomes still simpler by the absence of the uredinia. In *Puccinia Malvacearum*, the basidiospore develops a uninucleate mycelium which produces the telia where plasmogamy occurs. The fusion cells develop to short, branched, binucleate hyphae, each of whch forms a teliospore at its tip. This can germinate immediately to a basidium with basidiospores, which infect new hosts and again develop uninucleate mycelia with telia. In contrast to the long-cycled forms, this species is able to complete its life cycle several times within one season. These micro- forms, whose teliospores are capable of immediate germination, are sometimes placed in a special group called lepto- forms. Wintering over occurs by the delayed germination of teliospores. In other micro- forms, as *Puccinia Veronicarum*, two types of teliospores are formed (p. 576). The life cycle of the micro- type takes place according to the following scheme (the pycnia which are absent in *P. Malvacearum* are here added):

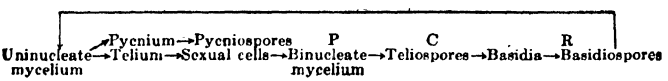


DIAGRAM XXXVI.

In *Uromyces Scillarum*, the scheme is modified so that plasmogamy occurs somewhere on the mycelium. This scheme is the same in principle as that assumed for the Septobasidiaceae. Still simpler is *Gallowaya pinicola*, where the teliospores are not formed as such, but each cell of the short binucleate chain resulting from plasmogamy divides directly after caryogamy to form a phragmobasidium. The vestigial pycnia are the only structures which distinguish it in principle from the simpler Auriculariaceae, since not even a resting organ, such as the probasidium, is formed.

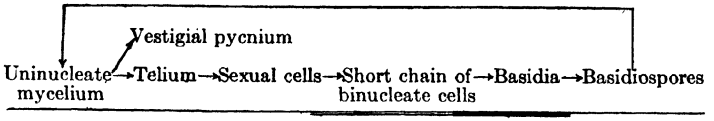


DIAGRAM XXXVII.

In these different developmental types, the following courses exist:

1. The plasmogamy is shifted in time and place. It occurs in the aecia of the eu-, -opsis and endo- forms (in *Uromyces Scrophulariae*, also somewhat on the mycelium) before the development of pycnia, in the uredinia of the brachy- forms, and in the telia or somewhere on the mycelium in the micro- forms. Characteristically, it occurs between two slightly differentiated hyphae or hyphal tips, in the former heterogamously by the migration of one nucleus to the other cell, in the latter

isogamously by the dissolution of the separating septum. It leads to the formation of a dicaryon which is adapted to multiple conjugate divisions.

2. In all forms the gonotocont (which characterizes the Uredinales as Basidiomycetes) is developed as a basidium which throughout the whole order has a stereotyped form (except for variation in length of sterigmata). In contrast to this fixity in form and function, it is very variable in place of occurrence. It can (in the Coleosporiaceae and *Ochropsora*) be formed directly on the mycelium; or it can (in the other three groups) germinate from the most bizarre, encysted or thin-walled teliospores; or it can develop from aeciospores which have arisen either in aecidium or caeoma. Throughout all these variations, it remains unaltered.

3. The sequence of the five spore forms is controlled by internal factors; it is irreversible. In the life cycle, one spore form or another may be degenerate or disappear entirely but there is no species known, parthenogenetic or apogamous, in which the sequence is changed. This innate regularity is based in part on the change in nuclear phase, in part on the great age of the Uredinales.

The only stable moment in the life cycle of the Uredinales depends on the fact that meiosis takes place in the same organ; on the other hand, the place of origin of the basidium and the place of the sexual act are variable. Furthermore, the gonotoconts are fixed in form (even to the basidium). The haploconidia (basidiospores and pycnospores) and the diploconidia (aeciospores and urediniospores) are fixed also. The zeugites (teliospores), on the other hand, are plastic.

Up to the present, in as far as we have discussed the bare fact of the ontogeny and morphology, the Uredinales agree with each other; there is, however, a complete anarchy in regard to the significance of all these forms and types of cycles. How have they arisen and how are they related? The answer to this question is difficult, for the Uredinales belong to the oldest known fungi and they have survived to our time, isolated as "living fossils." There exist today some very primitive genera but they are, for the most part, exotic and hence have not been investigated cytologically. Thus this answer cannot be given without considering at the same time the phylogeny of the Uredinales, their systematic division and the origin of their biological specialization.

Concerning the phylogeny of the rusts there are two concepts, that of Bary (1884) which derives the Uredinales from the Ascomycetes and that of Brefeld (1889) which connects them to the Zygomycetes. Many mycologists today, as Blackman (1904), Lotsy (1907), Dittschlag (1910), Kursanov (1910, 1922), Maire (1911), Fromme (1912), Mme. Moreau (1914), Gwynne-Vaughan (1922), Lindfors (1924) and, in part, Killian (1920) follow Bary's opinion; they consider the Uredinales as the most primitive Basidiomycetes and place them at the beginning of this class.

Their point of view rests mainly on structure of the male sexual organ, which has survived as the pycnium. This appears very similar to the "spermogonium" of the Ascomycetes, *e.g.*, *Polystigma;* furthermore, the formation of a sweet solution and the odor which is detectible by man may be considered as entomophily. Thus the pycnospores correspond extensively in form and size to the spermatia of the lichens; they possess, as these, large nuclei and very small amounts of cytoplasm and reserve materials. Also, up to the present, they have not been germinated at least to the stage of infection of the host.

The survival of the corresponding female organs would then be sought in the aecia. The ascomycetous ancestors had simple unicellular oogonia with unicellular trichogynes. The oogonia were joined together in groups and were fertilized by the spermatia arising in the spermatogonia. During the degeneration of sexuality, the spermatial fertilization disappeared and in its place two female oogonia copulated with each other. The survivors of these gametangia are the present palisade cells which may be regarded as a sorus of reduced female organs. The survivors of the trichogynes remain as sterile cells cut off at the top of the palisade cells; they have lost their function and have become buffer cells whose function is passive, *i.e.*, their dissolution gives the space necessary for the development of the spores.

Mme. Moreau (1914) has sought for a different significance for the aecia. She proceeds from the hypothesis of Dangeard of gametophores in the Ascomycetes. The present aecia were preceded by pre-aecia in which chains of female gametes ("pre-aecidiospores") were formed upon the basal cells ("gametophores"). Likewise, a series of male sexual cells were cut off in the pycnia. The male and female sexual cells passed into the open and copulated. Because of the degeneration of sexuality, the plasmogamy followed within the female gametophoric sori between two female gametes. The differentiation of gametes undergoes no interruption from this, only they are henceforth binucleate, behave no longer as gametes but divide into aeciospore and stipe cell.

These conceptions (assuming that the phragmobasidium is the original form of basidium) offer the advantage that they create in the Uredinales the sought-for link between the Ascomycetes and the Basidiomycetes; the latter had developed from the former through the rust series to the saprophytic forms. Other explanations, however, are possible. Thus, it is questionable whether the pycniospores are functionless spermatia, and accordingly under all conditions incapable of infection, since they are usually regularly and completely formed, even when in the microforms the other functional spore forms are suppressed. Here it is reasonable to suppose that for their further development they need the action of digestive juices of animals (Jaczewski, 1910). Even if they were functionless one could say more simply, that as diploconidia (urediniospores)

multiplied, the haploconidia became insignificant, except in *Gallowaya*, where they are vestigial although the haplont is dominant. If the pycnospores were spermatia it would be inconceivable why they should arise principally on the upper side of the leaf while the aecia which they should fertilize arise on the lower side, or that, *e.g.*, in *Cronartium ribicola*, they precede the aecia by at least one year (Colley, 1918; Adams, 1921). Furthermore in the Ascomycetes the functionless male sexual organs disappear before the female, hence it would be difficult to understand why their descendants would be unaltered and still form male sexual cells, capable of "germination" to a limited degree, while the female sexual organs, which continue to fulfill their function, are deformed beyond recognition. Furthermore in the development of the aecia, the homologizing of the sterile cells at the top of the palisade with the trichogyne, is not satisfactory.

Further, certain theoretical considerations contradict the direct derivation of the Uredinales from the Ascomycetes. In the ancestors among the Ascomycetes, it must have been a question of very primitive forms, *e.g.*, Silurian, in which the ascus was eight spored and still plastic. From this, in the course of time, the phragmobasidium of the Uredinales at present has developed so far that none of its variants may be referred to the ascus as an ancestral form. Vice versa, one must assume that the sexual organs which early became functionless were able to hold their own during this long course of development and even, in certain cases, to form sexual cells still capable of "germination." Such a conception is fundamentally improbable, for it is shown in all series of the Ascomycetes, particularly, that the sexual organs are especially liable to reduction, gradually become modified, degenerate and disappear entirely. In these changing forms, however, the gonotoconts, the asci, remain constant. From the Protascineae up to the highest Euascomycetes, they remain essentially the same in form and biological value, thus characterizing the Ascomycetes as a homogeneous group. If, however, one wishes to derive the Uredinales directly from the Ascomycetes, their development must have proceeded in the opposite manner. If the otherwise stable ascus has changed directly into a conidiophore, which does not resemble it even in spore number, while the otherwise variable sexual organs retained their ability to function and even to form sexual cells capable of germination, it is the first example of such an interchange in the phylogenetic law of continuity. This direct derivation of the Uredinales from the Ascomycetes, as significant as it was in its time, finds no support today.

B. O. Dodge (1924, 1925, 1926) develops an interesting modification of the hypothesis of the relationship of the Basidiomycetes to the red algae, which meets most of the objections raised against that hypothesis. Just as the Ascomycetous line is characterized by the gradual degenera-

tion and disappearance of the male organs and by the assumption of their function by vegetative fusions, in the Basidiomycetous line, the female organs disappear first leaving the male organs, no longer functional, as vestigial structures whose presence is still physiologically important[1] even after their cells have lost the corresponding female organs with which to copulate. The so-called sexual cells, gametes and sexual fusions are purely secondary, the fusions occurring between cells which are no more homologous to sexual organs, spermatia and oogonia, of any possible ancestral form than are the anastomoses of hyphae of the + and − strains of a heterothallic *Coprinus*. The presence of strains of rusts with a typical two-celled basidium, which is regularly associated with absence of spermogonia and the production of uninucleate spores, suggests that the presence of spermogonia may influence cell fusions in which they do not themselves take part, although a few cases have been observed where uninucleated spores have been produced in the presence of spermogonia.

There is something in the inheritance of the rusts that determines when and where these cell fusions shall take place, as well as the nature of the cells fusing. The five great orders in the Florideae are distinguished mainly on the basis of the form and disposition of the carpogonial branches and auxiliary cells, and on the nature of the cell fusions which follow as secondary events. The gonimoblasts or ooblastema filaments, sporophytic outgrowths from the fertilized egg, in many genera are also involved in these secondary fusions preliminary to the development of the carpospores. It is to these secondary cell fusions in which the auxiliary cells of the red alga take the leading part, that we must look for the homologues of the fusing cells of the rust.

There being no organ such as the egg apparatus in the rusts, the spermogonia, although they are so well developed in many species, can not carry out their primary male sexual function. Nevertheless there may be a series of activities in the growth of the rust linked with or influenced by the very inheritance which manifests itself morphologically in the shape of spermogonia. The fusions between the ooblastema filaments and auxiliary cells, and the other cell fusions in the red algae may very well be determined by the stimulus resulting from the presence of some of that element of maleness normally derived from the spermatium during fertilization. In the absence of the sexual fusions certain auxiliary cell fusions would not occur. Femaleness in the red algae outwardly expresses itself primarily in the organization of the carpogonial branch bearing the egg cell and its trichogyne. Auxiliary cells are secondary manifestations or accompanying phenomena. In a dioecious alga one should not expect to find auxiliary cells borne on the male plant. Femaleness in *Caeoma nitens*, *i.e.*, the power to develop an egg apparatus, has been lost. Auxiliary cells represented by the cells in the sorus primordium are the secondary expressions. These cells are capable of fusing, usually in pairs, under a certain stimulus.

[1] Unpublished experiments described in a letter from J. H. Craigie confirm this statement fully in *Puccinia Helianthi*, where the transfer of pycniospores from one pycnium to another appears necessary to secure normal development of aecia and binucleate aeciospores.

Maleness in the red algae is expressed in the form of antheridia producing spermatia. These bodies function primarily in fecundation and, in certain groups, secondarily in the cell fusions subsequent to fertilization. In the rusts maleness has persisted as shown by the development of spermogonia with their spermatia which are primarily functionless in the absence of an egg apparatus. This condition is associated with the occurrence of accessory cell fusions culminating, in *Gymnoconia*, in nuclear fusions in the teliospore.

A long-cycled rust becomes short cycled without losing the power to develop the basidium, which may be formed without previous caryogamy, in which case there is no necessity for meiosis. Therefore the number of cells in a phragmobasidium need not always be four. The presence of some male element exercising its secondary function indicates maturity, and plasmogamy will occur, while inhibition of such a development is shown by the absence of plasmogamy.

The Brefeld school (Brefeld, 1889; Tavel, 1892; Christman, 1907; Olive, 1908, 1911; in part E. Fischer, 1912) proceeds from the hypothesis discussed on page 421, that the basidium is a conidiophore which has become constant in form and spore number. Thus it connects the Uredinales and the Auriculariaceae with the Zygomycetes and attempts to elucidate this by a comparison between *Chaetocladium* and *Endophyllum*. The zygospores of *Chaetocladium* and the aeciospores of *Endophyllum* are both the direct product of a sexual act and both germinate normally with a conidiophore, which in *Chaetocladium* is indefinite and in *Endophyllum* is fixed as a basidium. The remaining spore forms were developed succesively *de novo*. This conception offers the advantage that it draws a direct parallel for the plasmogamy occurring between two basal cells and for the fusion cell itself: functionally the fusion cell is a zygospore formed by the copulation of gametangia which have become uninucleate. The difficulty is that it requires the basidium to be a stabilized conidiophore which, as has been shown on page 421, is contradicted by important cytological considerations. Therefore, between the organization of the Zygomycetes and of the Uredinales, there lies such a broad gulf that this conception would be untenable.

A third solution of the problem consists in the connecting of the Uredinales to other Basidiomycetes, particularly the Auriculariaceae. This idea was first expressed by Möller (1895) and further developed by Jahnchen (1923) and Neuhoff (1924). As a starting point one might consider Auriculariaceous forms, as *Eocronartium muscicola*, which possess micro- and macroconidia. The microconidia, cut off singly on unicellular sterigmata, are the ancestors of the pycniospores. The macroconidia arose singly from a mother cell which divided into a spore and a stipe cell, something as the initial cells of *Phragmidium Potentillae-canadensis* at the present time. With the transition to endoparasitism and the increasing difficulty to rupture the tissue of the host, the sporophores collect into sori.

Since plasmogamy took place originally, as in the Polyporales and the Agaricales, anywhere between two hyphal cells, its shifting in the life cycle of the rusts and the remaining cases of pseudogamy are explained. Because of their endoparasitism, the hyphae became limited to the narrow intercellular spaces where they generally found no mate. Hence it is not remarkable that plasmogamy took place (at first preferably and in time exclusively) where for the first time in the life cycle numerous parallel hyphae were pressed together, *i.e.*, in the primary uredinia of the ancestral forms. From these developed the more highly specialized aecia. This derivation is based on the fact that the urediniumpossessed both the single-spored type (in which the stipe cells have only one purport) and the chain type, which led directly to the aecia. It is also supported by the fact that in certain heteroecious forms, as *Puccinia Sydowiana* (*P. Vilfae*), *P. perdermiospora* and *P. Seymouriana*, the aeciospores show peculiarities of structure so similar to those of the urediniospores that Arthur assumes a genetic connection between the aecial mycelium and the uredinial mycelium on other hosts, which he has demonstrated by cultural experiments. According to this, the eu- type would have arisen from the brachy- type.

In connection with this localized pseudogamy the different groups of copulating hyphae may be explained; the types of *Puccinia Mariae-Wilsoni*, *P. Violae* and *Endophyllum Semperviri*, etc., are only special cases produced by the structure of their sorus. Where the separating wall is incompletely dissolved or only a pore is formed, plasmogamy is heterogamous; where the dissolution of the wall proceeds further and extends almost along the whole wall, the nuclear migrations become feeble and plasmogamy is isogamous according to the present terminology; these differences are not fundamental but only quantitative.

The abscission of sterile cells may be explained on this basis, as Mme. Moreau does. Copulation took place only after the basal cells had already cut off some spores, and had continued their activity as diploconidia.

From these points of view, one may represent the phylogenetic development of the Uredinales hypothetically in the following manner (Dietel, 1903, 1904, 1909, 1912, 1915, 1918; Faull, 1928): The primitive forms derived from the Auriculariaceae had lived on ferns in the Silurian. When the conifers appeared, its gametophyte could also live upon these. Subsequently the greater part of the cycle was shifted to the conifers upon which it developed greater dependence. They retained the gametophyte host and successively seized as suitable hosts those which, in the course of geological time, they encountered among the developing angiosperms. From a morphological viewpoint, they are characterized by the development of special zeugites which in the lower forms are formed at any point in the mycelium but in the higher forms arise in special sori and are transformed into teliospores. In the Coleosporiaceae and Melampsoraceae,

with the exception of *Melampsora* (to be considered later), they live in the haplophase exclusively on conifers, in the diplophase in different ferns and angiosperms.

The zeugites gradually lost their significance and hence were no longer retained in the families branching off the main line. The primary cause may be that, as today in *Hyalopsora* and *Uredinopsis*, the urediniospores are able to winter over; thus meiosis was in the course of time fixed at their germination in the spring, *i.e.*, the formation of the basidia was shifted forward to the overwintering urediniospores which thus assumed the role of zeugites and thereby attained new morphological developmental impulses.

At first there developed the Cronartiaceae whose urediniospores and teliospores are similar and whose teliospores contribute toward propagation. They retained the conifers as their gametophyte hosts.

Thus there proceeded a special permanent development from forms with the single-spore type of urediniospores, all the more so as their branching off went hand in hand with a period of mutation in respect to physiological requirements. That such physiological mutations can occur is supported by the example of *Cronartium asclepiadeum* whose sporophytes can infect both *Vincetoxicum*, *Paeonia* and *Pedicularis* (which appear in the north temperate zone, the home of the gametophyte host, the pine, and hence may be regarded as the true hosts) and various exotic angiosperms, Verbenaceae, Balsaminaceae, Loasaceae, Tropaeolaceae and Solanaceae, which it met for the first time in the course of experiments (Klebahn, 1914, 1916). A relaxation of extreme specialization must already have been encountered in *Melampsora*, the only genus of these three families which changed its gametophyte host by migrating either to the sporophyte host, *i.e.*, becoming autoecious, or to other angiosperms, Amentiferae, Saxifragaceae, Monocotyledoneae, etc. Besides the consideration set forth here, basidial formation is deferred to specially formed urediniospores from which arise the stipitate teliospores of the Pucciniaceae, no longer joined into crusts.

Thus the Pucciniaceae are apparently of recent date. Since the Amentiferae are not parasitized, they must have been formed later than these. The oldest forms were plurivorous (omnivorous) and attained a full development at the time when the earth was being covered with a mass of new angiosperm families. The purely autoecious forms attained a prolific development in the tropics and the south temperate zones especially on Leguminosae, and in the north temperate zone chiefly on Rosaceae. There they have divided into a whole series of morphologically distinct genera of which, on Leguminosae, we have mentioned *Uromycladium* and *Ravenelia* and on Rosaceae *Phragmidium*, *Ochropsora*, *Triphragmium*, *Kuehneola* and *Gymnoconia*. Also the partially heteroecious *Gymnosporangium* has possibly arisen from this group by a second

shifting of the gametophyte from Rosaceae to conifers. Their teliospores usually resemble those of *Phragmidium*.

The remaining mixed genera which contain both autoecious and heteroecious species, particularly *Uromyces* and *Puccinia*, in contrast to the Coleosporiaceae, Melampsoraceae and Cronartiaceae, are distinguished in their change of host by a great stability in their sporophyte which chiefly inhabits the Glumiflorae, while their gametophytes have been spread to more than 50 families of angiosperms and again have become largely specialized to specific hosts. From these species, by a reduction of the life cycles, have arisen numerous micro- and endo- forms (E. Fischer, 1904, 1910; Dietel, 1918). In the micro- forms, meiosis came about in the long-cycled species as a result of a simplification of the life cycle where all spore forms up to the teliospore and eventually the pycnia were suppressed. In other cases there must have taken place a shifting of place of teliospore formation; thus the telia discussed on page 568 of *Puccinia Fergussoni* on *Viola* do not coincide with the structure of telia but with the aecia of the corresponding eu- form, *Puccinia Violae*, and in *Uromyces scutellatus*, *U. laevis* and *U. alpestris* on *Euphorbia* (mentioned on p. 568). Altogether one obtains the impression that the sorus was originally developed as an aecium, later became indefinite and was merged with the telia. These forms appear chiefly in tropical, alpine and polar regions.

The development in the endo- forms has proceeded a step further; here also caryogamy has been advanced into the aecium, occurring in aeciospores rather than teliospores. While in the micro- form, *Uromyces alpestris*, teliospores are formed within the sori, originally considered to be aecia, where caryogamy takes place, in the endo- form, *Endophyllum Euphorbiae-silvaticae* on *Euphorbia*, the original tendency of the sori to form aeciospores preponderates and caryogamy takes place there. According to this conception the endo- forms are the end members of a series of developments which, by shifting of teliospore formation in certain micro- forms, became introduced into the aecium. Both *Endophyllum* (with aecidia) and *Kunkelia* (with caeomata) may thus be considered, not as natural monophyletic genera, but as biological groups similar to the brachy- and hemi- groups. As an initial impulse for these modifications, we may consider a migration of the mother species into warmer regions. Thus the ancestral form on *Rubus*, *Gymnoconia Peckiana*, is found in the colder regions of North America, while its apparent derivative, the endo- form *Kunkelia nitens*, also on *Rubus*, is found in the warmer regions of the South and West. Besides, the number of endo- forms known from the tropics is continually increasing. In connection with this degeneration have again arisen forms in the Pucciniaceae quite similar to the primitive forms and consequently were considered primitive by many authors (E. Fischer, 1912; Groves, 1913).

As in the other orders, the probable relationships between the families and genera have been schematically represented below.

In conclusion there may be briefly cited from the four families some interesting, pathologically important species, whose nomenclature, because of the various estimates of their biological importance, is always in a state of flux. The gametophytes of the Coleosporiaceae, Melampsoraceae and Cronartiaceae occasionally produce pandemic diseases of conifers. Their aecidia are designated as blister rust, and earlier, when their heteroecism was unknown, were grouped together in the single genus *Peridermium*. In the gametophyte, the species of *Coleosporium* live on

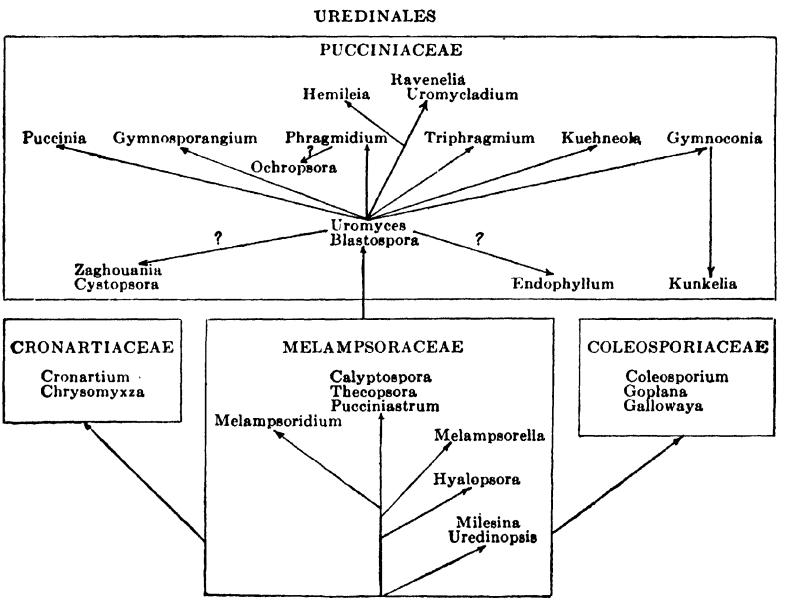


DIAGRAM XXXVIII.

pine needles; their sporophytes are specialized on different angiosperms as that of *C. Sonchi* on *Sonchus*. *C. Senecionis* and *C. Campanulae*, besides growing on their normal sporophyte hosts (*Senecio* and *Campanula* respectively), also attack representatives of exotic families. In *Chrysomyxa* the micro- form, *C. Abietis* lives on fir needles, in the gametophyte; the heteroecious eu- form, *C. Rhododendri* lives on *Rhododendron* in the sporophyte. *Cronartium ribicola*, the white pine blister rust, has its gametophyte on the bark of *Pinus Strobus* and other white pines, the sporophyte on *Ribes*. *C. asclepiadeum* causes blister rust of the pine, while its sporophyte is plurivorous (p. 592). *Melampsora pinitorqua* causes a disease of pines (gametophyte on *Populus*) and *Melampsorella*

elatina (*M. Caryophyllacearum*), the witches' broom of the white fir (sporophyte principally on *Stellaria* and *Cerastium*).

Among the autoecious species of Pucciniaceae are *Uromyces Betae*, the beet rust, *U. appendiculatus* (*U. Phaseoli*), the bean rust, *Hemileia vastatrix*, the coffee rust, and *Phragmidium disciflorum* and its relatives, the rosaceous rusts; among the heteroecious forms are *Puccinia, Pruni-spinosae*, the plum rust (gametophyte on Ranunculaceae), *Puccinia graminis*, the highly specialized black rust of cereals and other grasses (gametophyte on *Berberis vulgaris* and its relatives), *P. dispersa*, the brown rust of rye (gametophyte on Borraginaceae), *P. triticina*, the brown rust of wheat (gametophyte on *Thalictrum*), *P. glumarum*, the yellow rust of cereals (gametophyte unknown), *P. Lolü* (*P.*) *coronifera*, the crown rust of oats (gametophyte on *Rhamnus*) and *Gymnosporangium Sabinae*, *G. globosum* and *G. Blasdaleanum*, the rust of apples and pears (sporophyte on *Juniperus* or *Libocedrus*).

CHAPTER XXXIV

USTILAGINALES

The Ustilaginales, or smuts, include several hundred species which parasitize higher plants, develop their thick-walled spores (smut spores) in definite organs and impart to these organs a burnt or charred appearance. In contrast to the Uredinales, they are saprophytic in a portion of the life cycle, and some of them may complete the whole cycle in artificial culture.

Their mycelium consists of slender, hyaline hyphae whose cells, corresponding to the cytological life cycle, in some species are uni-, in others binucleate; occasionally, as in the higher Basidiomycetes, they can become multinucleate (Fig. 397, 1). In some forms, as in the corn smut *Ustilago Zeae* (*U. Maydis*) and in *Entyloma* and *Doassansia*, they grow only in the region of initial infection (*i.e.*, in all the growing parts of the plants, even the roots) where they form their sori. In most other forms they penetrate the whole plant or single sprouts and much later form sori in leaves or fruits. *Ustilago Tritici*, the loose smut of wheat, and *U. nuda*, the loose smut of barley, infect flowers; the mycelium winters in the seeds, grows behind the growing point the following year and, at the end of the growing season, it forms a sorus in the ear. In most other cereal smuts, as *Tilletia Tritici*, bunt of wheat, *U. Avenae*, the loose smut of oats, *U. levis*, the covered smut of oats, *U. Hordei*, the covered smut of barley, *U. Crameri*, the millet smut, and *Tuburcinia occulta* (*Urocystis occulta*), the stem smut of rye, the infection takes place in spring in the young seedlings, the mycelium grows up the stem behind the growing point and forms the sorus: in *T. Tritici* and *U. Crameri* in the ovary; in *U. Hordei* in the ears; in *U. Avenae* and *U. levis* in the panicle; in *Tuburcinia occulta* mainly in the stem and leaves. In *Cintractia Caricis* and *Tuburcinia Trientalis* the mycelium is perennial in the rhizome and the shoots. In the former, it forms the sorus in the ovary, in the latter in the stems and leaves.

The hyphae are mostly intercellular; in some species, as in the Uredinales, for the sake of nourishment they penetrate the host cells with capitate or racemoid haustoria and thereby cause direct injury to the plant. Thus the specimens of *Trientalis* infected by *Tuburcinia* are recognizable by the pathological thickening of their stems and the smaller size and lighter color of their leaves. In *Entyloma Nymphaeae* the haustoria arise as special branches of the intercellular hyphae and swell

into multinucleate appressoria, as in the Erysiphaceae, before the penetration of the host cell (Lutman, 1910). In many other forms, *e.g.*, in most of the cereal smuts, the hyphae are only intercellular parasites, form no haustoria and take their food directly by osmosis. Even in these, however, the decomposition products of the hyphae seem to cause injury to the host, *e.g.*, in *Tilletia Tritici* a retardation of growth and increased susceptibility toward *Puccinia glumarum* (Lang, 1917). In still others, *e.g.*, *U. Zeae*, the hyphae grow intracellularly, penetrate the individual host cells and cause death.

Conidia are formed on the host in some genera, as *Entyloma* and in *Tuburcinia Trientalis* (Woronin, 1881) and *Ustilago Vuijckii* (Seyfert, 1927). The hyphae form thick, white mats of simple unbranched conidiophores on the lower sides of the leaves between the epidermal cells or on the filaments which creep around on the epidermis. The conidiophore repeatedly cut off hyaline pyriform conidia which germinate with germ tubes or, under unfavorable conditions, with secondary conidia.

In most other genera only the smut spore is known. It develops in certain organs of the host and only on its appearance may the infected plants be recognized as such. In many species, the host is not further deformed by the formation of a sorus. The tissue in which spore formation proceeds is resorbed; thus wheat kernels infected by *Tilletia Tritici* are recognizable by a slight swelling, a darker color, and a greater spreading of the glumes. Because of the presence of trimethylamine in the smut spores, their intense odor is like that of herring brine. Other species cause characteristic hypertrophies; thus the ovule of *Polygonum Hydropiper* attacked by *Sphacelotheca Hydropiperis* is turned into a spore "capsule" which often extends far above the unaltered perianth and, at maturity of the spore, bursts open in valves. In *Melandryum* the female flowers are induced to form staminate filaments by *Ustilago violacea* which, as *U. Scabiosae*, forms its sorus only in the anthers. These filaments are colonized by the fungus and destroyed. In *U. Zeae*, the parenchyma of the host is stimulated to form gelatinous growths up to the size of a child's head (smut tumors), which are again dissolved by the fungus. In eastern Asia the natives eat as vegetables beet-like stems of *Zizania latifolia* deformed by *Ustilago esculenta* (Hori, 1907); and in *Polygonum chinense* of Java the stem is stimulated by *Ustilago Treubii* to growths which occasionally appear like *Cantharellus* and form in their interior a peculiar capillitium which apparently participates in the dissemination of spores. The number of the spores formed in such a sorus is very large; in *Tilletia Tritici*, it averages four million spores per smutted kernel; according to Buller (1909) even twelve million.

The smut spores, as the teliospores of the Uredinales, arise exclusively on binucleate mycelia. Before their formation the hyphae branch very much and form thick tissues of extremely slender, small cells which, as a

result of the swelling of their membranes, lie imbedded in a gelatinous sheath. In *Ustilago Tragopogonis-pratensis* (Rawitscher, 1912) and in *U. Heufleri* (Sartoris, 1924), they divide into short unicellular sections which become moniliform and loosen themselves from the cell chain. They are irregularly angular (Fig. 397, 8 and 9), subsequently round off and change to thick-walled spores whereby the dissolved membranes are resorbed. In *Entyloma Nymphaeae* (Lutman, 1910) the sporogenous hyphae form numerous short side-branches, each of which develops a terminal spore (Fig. 394, 4 to 8). In *Neovossia*, at least in *N. Moliniae*, the proximal part of the sporiferous branch becomes thickened and remains as an appendage of the mature spores (Fig. 401, 3 to 5). In

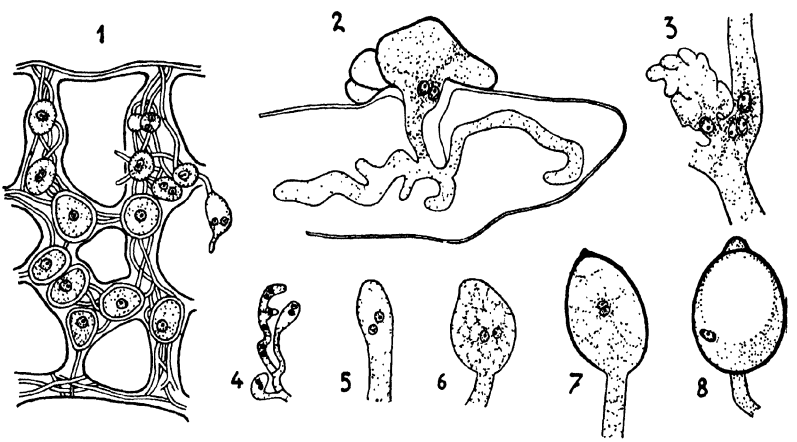


FIG. 394.—*Entyloma Glauci*. 1. Sorus of smut spores. *Entyloma Nymphaeae*. 2. Section of haustorium. The old appressorium has thickened its wall. 3. Young appressorium with nuclei entering. 4 to 8. Development of smut spores. (1 × 500; 2, 4 to 8 × 1,600; 3 × 860; *after Dangeard*, 1892, *and Lutman*, 1910.)

Cintractia, the spores are successively cut off from a columella-like stroma which covers the ovary; they are progressively pushed outward and at maturity increase very much in circumference, adhere more or less securely and flatten into irregular polyhedra. In most forms the mycelium is entirely used up by spore formation and dissolved by the swelling; in *Cintractia* an unused part remains within the spore mass.

The smut spores are hyaline and binucleate when young; in the course of development the dicaryon fuses to a single diploid nucleus (Fig. 394, 4 to 8). The mature spore wall consists of a thin endospore and a brown or violaceous, often characteristically sculptured exospore. In many genera of the Ustilaginaceae, *Sphacelotheca*, *Ustilago* (Fig. 395) and *Cintractia* (Fig. 397, 6) and of the Tilletiaceae, in *Tilletia* (Fig. 399), *Neo-*

vossia (Fig. 401) and *Entyloma* (Fig. 394, 8) and in the Graphiolaceae, the spores arise singly and form a dusty mass at maturity. In *Entyloma*, they remain in the interior of the host, joined into small, light-colored nests which germinate *in situ*. In *Sphacelotheca* the spore fundaments are only changed to real spores in the middle layers of the sorus; toward the outside and the interior their formation is incomplete; they remain colorless, adhere in a tissue and form a five- to ten-celled hyaline sheath which covers the true spores on both sides.

In other genera, among the Ustilaginaceae, *Tolyposporium*, *Thecaphora*, *Testicularia* and in the Tilletiaceae, *Tuburcinia* and *Doassansia*, several or more spores are joined into a spore ball. In *Tolyposporium*, *Thecaphora* and *Tuburcinia* (Fig. 400, 4 to 6), all spores are fertile. In Fig. 402, 4, *Doassansia* (Fig. 403, 4 and 5, 9 to 11) the outer spores degenerate, lose their nuclei and contents and remain hyaline. In *Testicularia* the spore ball consists of an outer fertile layer, surrounding an inner ball of pseudoparenchyma. In *Tuburcinia*, the spore ball results from repeated division of one or more cells from the same hypha; in *Doassansia*, the whole hyphal tissue of an intercellular space or breathing pore becomes changed to a large ball resembling a seed, whose outer cells form an almost complete sheath, which, after the decay of the host tissue, makes it possible for the ball to float on the surface of water. The smut spores are generally disseminated by wind or insects; more seldom, as in *Doassansia*, is the whole ball borne by water. They are mostly capable of germination without a rest period but retain the ability to infect for several years. Germination takes place in water, more freely in dilute nutrient solutions; the exospore bursts open and a germ tube whose wall is a continuation of the endospore protrudes. Germ pores are known in only a few forms, *e.g.*, *Ustilago Tritici*. The further course of germination is used to separate the Ustilaginaceae and the Tilletiaceae.

Ustilaginaceae.—Typical examples are *Ustilago Scabiosae* (Harper, 1898), *U. Tragopogonis-pratensis* (Dangeard, 1892; Federley, 1904; Rawitscher, 1912), *U. violacea* (Dangeard, 1892; Harper, 1898; Werth and Ludwigs, 1912), *U. Zeae* (Rawitscher, 1912), *Sphacelotheca Hydropiperis* (Brefeld, 1895), *U. Heufleri* on *Erythronium americanum* (Sartoris, 1924) and *Testicularia Cyperi* (Edgerton and Tims, 1926). When the germ tube (promycelium) has attained about one-third its final length, the diploid nucleus migrates into it (Fig. 395); when the promycelium is fully developed, it divides meiotically, forming three septa. In rarer cases the nucleus remains in the spore and divides there; in this case one daughter nucleus migrates to the promycelium, divides and a septum is formed between the promycelial nuclei. The distal promycelial cell may divide again, producing a three-celled promycelium. In contrast to the basidium of the *Auricularia* type, the promycelial nuclei do not slip out into the basidiospores but remain in the promycelium. By lateral

and terminal growth, these spores develop indefinitely into easily dissociable sprout mycelia (Fig. 395, 4, 8 and 9), with slightly ellipsoidal, uninuclear cells, which continue budding until food is exhausted. In *U. violacea* and *Testicularia Cyperi*, the whole promycelium may be loosened from the smut spore and, lying free in the nutrient solution, may sprout further. When the food is exhausted, the sprout cells form long fine filaments on the surface so that in some forms, as *U. zeae* (Fig. 396, 2 and 3), a white pellicle results (Brefeld, 1895). From a definite moment, *i.e.*, at a certain oxygen tension of the medium (Bauch, 1922), the sprout cells copulate either directly or through copulation tubes (Fig. 395, 10 and 11). Descendants of the same promycelial cell, at least in *Ustilago violacea*, do not copulate with each other. The four tetracyte nuclei are sexually differentiated in pairs. Apparently each nucleus impresses on its cell a definite sexual character, thus causing the formation of copulation tubes (Kniep, 1919). In the form of *U. violacea* on *Dianthus deltoides*, there appear secondary sexual characters which distinguish the sprout mycelia of both sexes by the physiological peculiarities of their behavior toward albumoses, peptones and disodium phosphate (Bauch, 1922). The sprout cells, which become binucleate, bud further with conjugate division of their nuclei until they reach a suitable host, within which they form germ tubes and develop to binucleate mycelia which in turn form sori in the "predestined" organs.

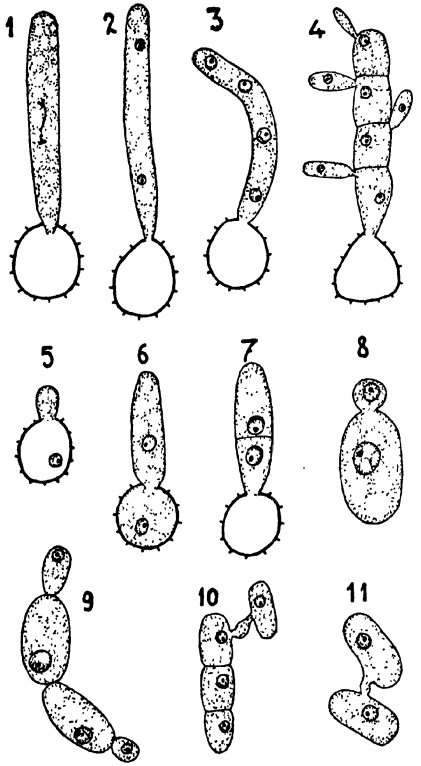


FIG. 395.—*Ustilago Scabiosae.* 1 to 4. Germination of smut spores. *Ustilago violacea.* 5 to 7. Germination of smut spores. 8, 9. Sprout mycelium. 10, 11. Copulation of sprout cells. (1 to 7, 10, 11 × 1,000; 8, 9 × 1,500; *after Harper*, 1898.)

U. Zeae and *U. Vuijckii* form an important exception to this scheme. Here the sprout cells do not copulate, hence the hyphae within the host are uninucleate and plasmogamy first takes place in the sorus (Rawitscher, 1912, denied by Seyfert, 1927). The gelatinous denticulate portions

of a sporogenous hypha lie beside each other in pairs (Fig. 396, 4 to 9), the separating walls dissolve and nuclei migrate toward the middle, while both sides become thinner and emptier; generally they can still divide into two daughter cells. They then round off, thicken their walls and, with the fusion of the dicaryon, are transformed to smut spores.

These figures of germination in Figs. 395 and 396 are of the *Ustilago Scabiosae* type and are extensively modified in many other forms of the Ustilaginaceae. In *U. domestica* (Fig. 397, 11), on *Rumex domesticus*, and U. *Holostei* (Fig. 397, 10), sprout cells are formed only on two promycelial cells, where many are present in whorls. In *U. domestica* they

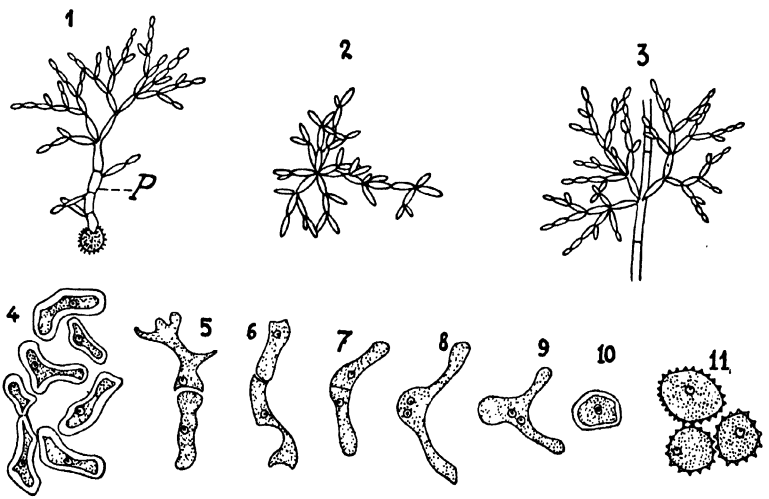


FIG. 396.—*Ustilago Zeae*. 1. Germinating smut spore. Promycelium, *P*, developing a sprout mycelium. 2. Sprout mycelium. 3. Hypha with sprout cells. 4. Uninucleate hyphae from a lesion on corn. 5, 6. Uninucleate hyphal cells. 7 to 9. Copulation. 10. Young spore. 11. Mature uninucleate spores. (1 to 3 × 300; 4 to 11 × 660; *after Brefeld*, 1895, *and Rawitscher*, 1912.)

copulate as soon as they have fallen away; in *U. Holostei* the upper ones grow downwards clinging close to the promycelium, the lower ones grow upwards and copulate without falling off. Only the binucleate sprout cells fall away and germinate to sprout mycelia (Brefeld, 1895). From analogy to *U. violacea*, we must assume that the promycelial cells are sexually differentiated.

In *Cintractia Montagnei* on *Rhynchospora*, the promycelium is four celled (Fig. 397, 6 and 7), the lower cell generally remaining in the spore (Rawitscher, 1922). Immediately after the formation of septa, or almost simultaneously, each pair of neighboring cells copulates either by resorption of the wall or by copulation tubes; the content of one cell does not

migrate into the other but the copulation tubes take up the contents of both cells and develop to sprout mycelia.

In other species, as *U. nuda* (Rawitscher, 1922), *U. Tritici* (Lang, 1910; Paravicini, 1917) and *U. Hordei* (Hils, 1912), the promycelium, under suitable conditions of growth, *i.e.*, in presence of high oxygen tension, may develop mostly to unbranched hyphae instead of sprout mycelium. Occasionally these hyphae can again change to sprout mycelium. Between two more or less neighboring hyphal cells or between two hyphae of different promycelia, there appear copulation tubes through which the content of one cell wanders over into that of the other.

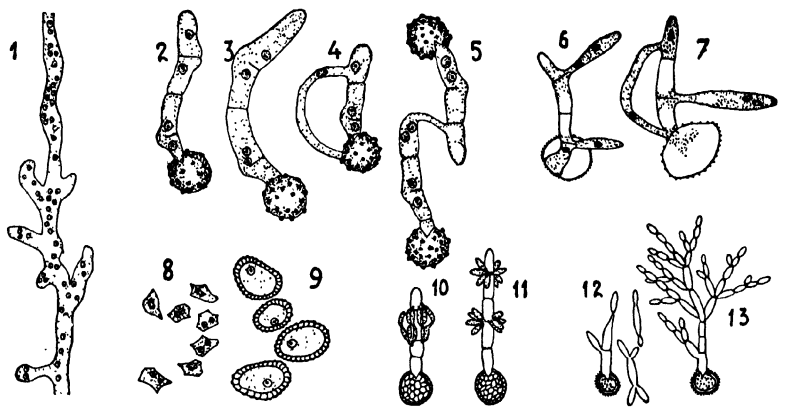


FIG. 397.—*Ustilago levis*. 1. Portion of intercellular hypha. *Ustilago nuda*. 2 to 5. Germinating and copulating promycelia. *Cintractia Montagnei*. 6, 7. Germinating and copulating promycelia. *Ustilago Tragopogonis pratensis*. 8. Young binucleate spore fundaments. 9. Mature uninucleate spores. *Ustilago Holostei*. 10. Germination of smut spore with fusing sporidia. *Ustilago domestica*. 11. Germination of smut spore in nutrient solution. *Ustilago Panici-frumentacei*. 12. Submersed germination of smut spore. 13. Germination of smut spore in air. (1 × 860; 2 to 9 × 660; 10 to 13 × 240; *after Lutman*, 1910; *Rawitscher*, 1912, 1922; *and Brefeld*, 1895.)

In *U. bromivora* (Bauch, 1925), as in *Cintractia Montagnei*, copulation may occur between two promycelial cells through copulation tubes or, as in *U. violacea*, between two ordinary sprout cells; in certain strains the sprout cells, as in the promycelial cells of *U. nuda*, develop first to long copulation tubes which only fuse at the tip. *U. bromivora* shows an interesting retrogression in the form of its promycelium. Besides the normal four-celled promycelium, there may also develop from a smut spore, two two-celled or one two-celled and two one-celled or one one-celled and one three-celled promycelium. The number four of the promycelial cells generally remains constant, while the promycelium has entirely lost its characteristic form.

This degeneration goes still further in *U. Panici-frumentacei;* where the promycelium is no longer four-celled but only two-celled. The distal cell is generally elongated and germinates to a sprout mycelium (Fig. 397, 12 and 13).

In still other species, *e.g., Thecaphora deformans* on Leguminosae, in *U. Vaillantii* on *Scilla, etc.,* and *U. longissima* on *Glyceria,* no true promycelium is formed. In *Thecaphora deformans,* the smut spores germinate in nutritive solutions to much-branched mycelia which cut off sprout cells (one apiece?) on dichotomous tips. These fall away easily and develop to new mycelia. On germination of the smut spores of *U. Vaillantii* in water, there emerge slender, uninucleate, germ tubes which

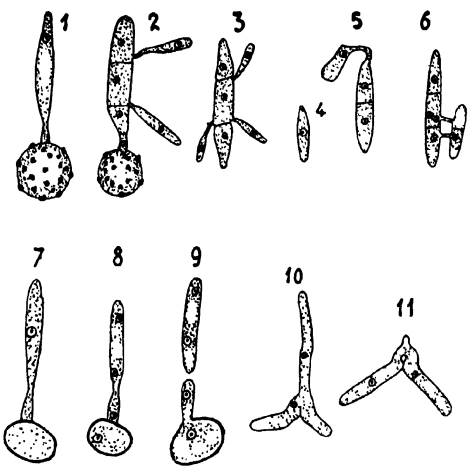


FIG. 398.—*Ustilago Vaillantii.* 1 to 6. (× 1,300.) *Ustilago longissima,* var. *macrospora* 7 to 11. Germination of smut spores (× 1,100). (*After Paravicini,* 1917, *and Bauch,* 1923.)

grow further. Their fate is unknown. On germination in nutritive solutions the germ tube remains very short and cuts off one or more sprout cells which generally fall away (Fig. 398, 2 to 4). The nucleus divides in three and forms two septa. The three-celled sprout mycelium cuts off at its septa further sprout cells which again become three-celled, etc. In older cultures, copulation takes place (Fig. 398, 5 and 6) either by copulation tubes or between different sprouts or by partial and temporary solution of the wall between two cells of the same sprout. The binucleate cells develop to slender hyphae (Paravicini, 1917). In *U. longissima* the germ tube develops to a multicellular, uninucleate mycelium which is easily broken up and proceeds to sprouting. The sprouts are again

indefinite in length and cell numbers. Under suitable conditions, copulation takes place through copulation tubes, whereupon their cells become binucleate and grow further by sprouting (Brefeld, 1883; Paravicini, 1917; Bauch, 1923). In the variety *macrospora*, meiosis occurs in the smut spore; the first sprout cell contains two nuclei of different sexual tendencies which generally are separated by a septum (Fig. 398, 9). The sprout cells arising from these are uninucleate (Fig. 398, 10 and 11) and copulate normally later (Bauch, 1923).

Tilletiaceae.—In *Tilletia Tritici* (Dastur, 1921; Rawitscher, 1922) meiosis takes place in the smut spore, as in *U. longissima* var. *macrospora*, and proceeds very rapidly, but not quite simultaneously. Generally there are three steps of division, forming eight daughter nuclei in the smut spore (Fig. 399, 1 to 7). Frequently some nuclei divide still further, whereby are formed from ten to sixteen nuclei. The nuclei first lie together in a sphere in the center of the cell and migrate into the promycelium which has been formed in the meantime. This is aseptate and on germination in damp earth is, very short; in a nutrient solution, it develops to a long thread whose base emits its protoplasm into the growing tip and remains empty (Fig. 399, 8); thereupon the empty parts are successively separated by septa. When the promycelium reaches the surface, a number of acicular sporidia corresponding to the nuclear number are cut off at the tip. Each sporidium contains a nucleus which subsequently is separated by a septum (Fig. 399, 9). While they still are attached to the promycelium or after they have fallen away, they copulate by tubes and the nucleus and cytoplasm of one migrates into the other. The sporidia which have become binucleate develop by conjugate division of their nuclei to slender mycelia which cut off large, thin-walled, binucleate, falcate conidia (Fig. 399, 10). These may again develop mycelia which finally penetrate into the delicate tissue of the seedling.

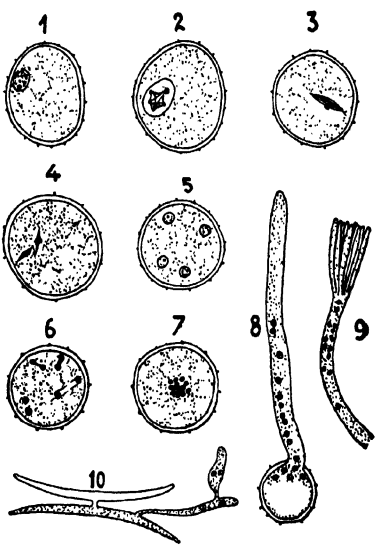


FIG. 399.—*Tilletia Tritici*. Germination of smut spores. (1, 6, 7, 10 × 660; 2 to 5 × 1,000; 8, 9 × 500; *after Rawitscher*, 1922, *and Paravicini*, 1917.)

The remaining forms of the Tilletiaceae correspond with the above picture of germination. In *Tuburcinia Trientalis* (Fig. 400, 7 to 11), the terminal cells of the promycelium fall away from the germ tube and

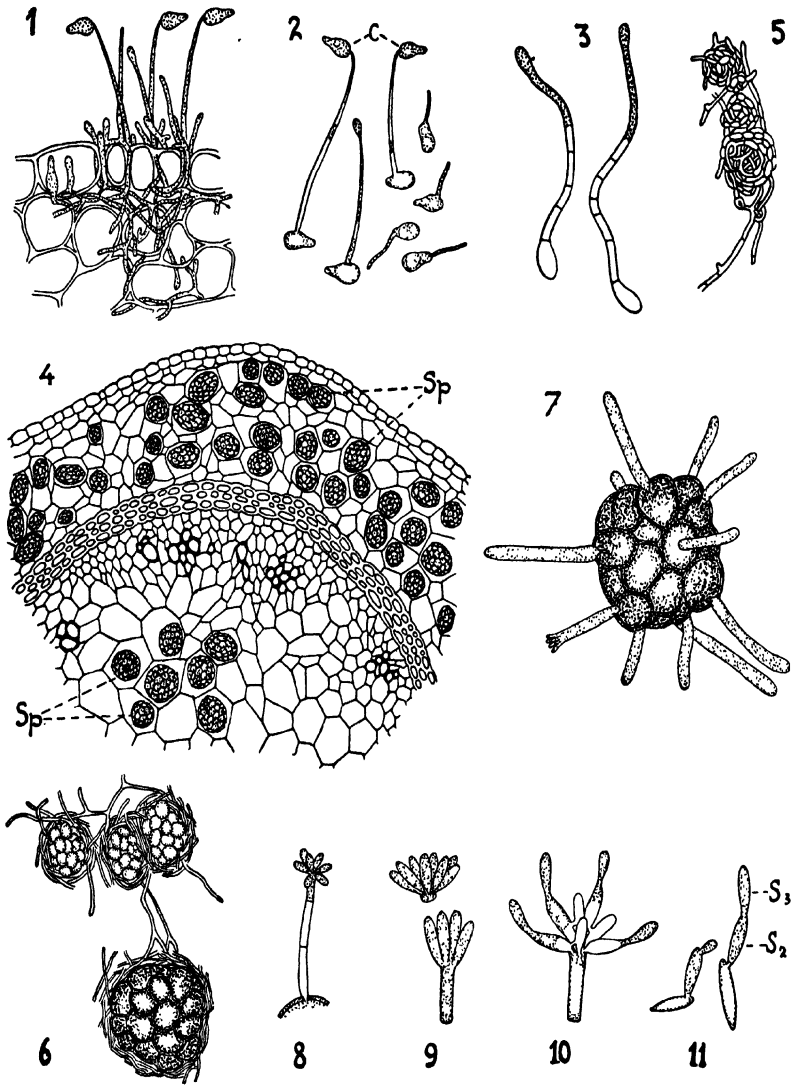


FIG. 400.—*Tuburcinia Trientalis*. 1. Section through an infected leaf. The conidiophores force their way between the epidermal cells. 2. Conidia germinating to secondary spores, *c*, in damp air. 3. Conidia germinating in water at the end of six hours. 4. Section through a stem, showing spore balls, *Sp*. 5, 6. Development of a spore ball. 7. Germinating spore ball. 8. Normal promycelium. 9. Basidial cells with four or eight basidiospores which have separated from the promycelium. 10. Later stage with copulation completed. 11. Sporidia germinating with secondary and tertiary spores. (1, 2, 5, 6 × 215; 3, 7, 8, 11 × 345; 4 × 60; 9, 10 × 415; *after Woronin*, 1881.)

the spore which collapses (Woronin, 1881). In *Neovossia*, from 30 to 50 or more sporidia are formed (Fig. 401, 4 and 5); they never fuse but

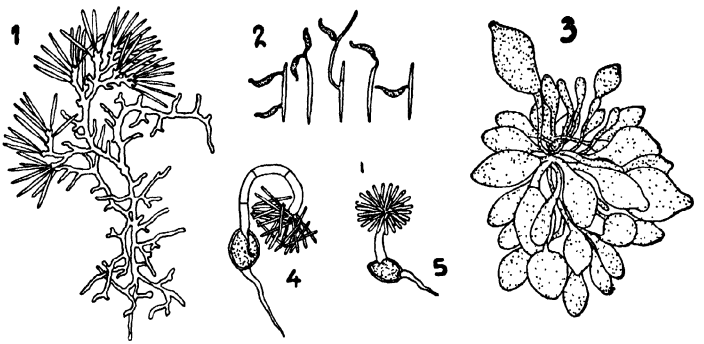


FIG. 401.—*Neovossia Moliniae*. 1. Tuft of hyphae with filamentous conidia. 2. Filamentous conidia germinating to falcate conidia. 3. Young smut spores. 4, 5. Germination of smut spores. (1, 2 × 270; 3 × 330; 4, 5 × 240; *after Brefeld*, 1895.)

develop to very slender mycelia which, in case the germination occurs in water, pour out their content into falcate conidia or, if the germination

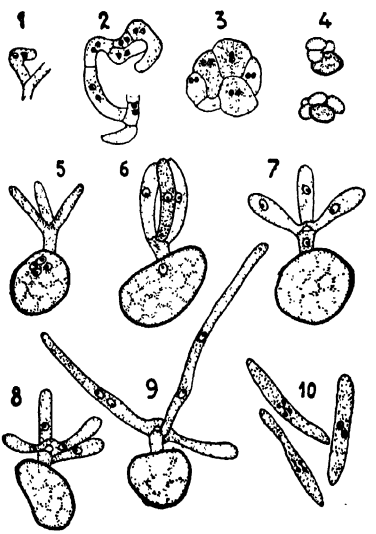


FIG. 402.—*Tuburcinia Ranunculi*. 1 to 3. Development of a spore ball with fertile and sterile cells. 5 to 9. Germination of smut spores. *Tuburcinia Violae*. 10. Binucleate sporidia. (1 to 3 × 860; 4 × 230; 5 to 9 × 450; 10 × 660; *after Lutman*, 1910; *Kniep*, 1921; *and Rawitscher*, 1922.)

takes place in nutrient solution, develop branched mycelia which, according to cultural conditions, form acicular or falcate conidia (Brefeld,

1895). In *Tuburcinia Ranunculi* (*Urocystis Anemones*) on *Ranunculus* (Fig. 402, 5 to 9) there are four daughter nuclei, eight in *Tuburcinia Violae*. The promycelium of the former divides into a whorl of three to four branches, in the latter into eight, which separate by septa. In case only three branches are formed, the fourth nucleus remains in the promycelium. Each two branches form two short outgrowths which come together in horseshoe-shaped copulation tubes. In individuals

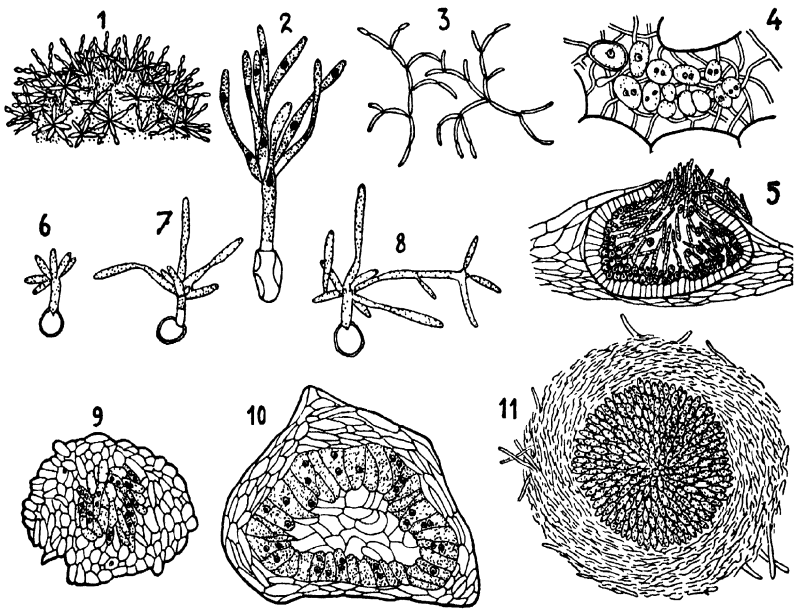


FIG. 403.—*Doassansia Sagittariae*. 1. Portion of a germinating spore ball. 2. Germination of smut spore and sprouting of conidia. 3. Sprouting of sporidia in nutrient solution. *Doassansia Alismatis*. 4. Development of a smut sorus. 5. Germinating spore ball. *Doassansia punctiformis*. 6 to 8. Germination, copulation and formation of sprout cells. *Doassansia deformans*. 9, 10. Development of a spore ball. *Doassansia Martianoffiana*. 11. Young spore ball. (1 × 100; 2, 4 × 500; 3, 6 to 8 × 245; 5 × 200; 9, 10 × 860; 11 × 440; *after Setchell*, 1892; *Dangeard*, 1892; *Brefeld*, 1895; *Lutman*, 1909; *and Rawitscher*, 1922.)

with three branches, the third branch copulates with the promycelium. In this manner there are formed from the four and eight uninucleate sporidia two and four binucleate sporidia (Kniep, 1921; Rawitscher, 1922). The binucleate sporidia develop to long, narrow hyphae, where the protoplasm and nuclei migrate toward the tip and are abjointed from time to time at the base; gradually in aqueous cultures, development ceases as a result of inanition. In special nutritive solutions after a few

weeks in *T. Ranunculi* there appear many little flakes of ramose hyphae. They gradually become gray brown and, on forming smut spores, dark brown.

In *Entyloma*, germination is similar to *Tuburcinia*, only in case copulation still occurs on the promycelium, copulation tubes are formed at the tips rather than at the base of the sporidia.

In *Doassansia*, finally, there are, as in *Ustilago*, two types of development: *D. punctiformis* on *Butomus umbellatus*, and *D. Alismatis* (Fig. 403, 6 to 8) behave as *Ustilago Scabiosae*, *i.e.*, copulation takes place between each pair of sporidia (Brefeld, 1895). In *D. Sagittariae* the sporidia germinate without copulation to uninucleate sprout mycelia (Fig. 403, 2 to 3) which after infecting the host continue as uninucleate mycelia. Copulation occurs, as in *U. Zeae*, on the formation of the smut spores (Rawitscher, 1922; Seyfert, 1927). *Tuburcinia primulicola*, known only from a short note by Wilson (1915), is exceptional. Its mycelium consists of uninucleate cells which winter in the host. It develops in the inflorescence and forms large masses of uninucleate conidia on the calyx. These fall off, lie on the corolla and copulate by tubes. The nucleus of one conidium migrates into the other. These binucleate cells germinate on the flowers to binucleate mycelia on which the smut spores appear later.

Graphiolaceae.—For a long time this family was shifted between the Phacidiales, Pyrenomycetes, Myxomycetes, imperfects and Ustilaginales, and has only recently been shown as undoubtedly related to the Ustilaginales (E. Fischer, 1883, 1920, 1922; Killian, 1924). The best-known representative, *Graphiola Phoenicis*, grows on the fronds of *Phoenix dactylifera*. Its fructifications appear on both the upper and lower sides of the pinnae, seldom on the midrib and form round or elongate, black tuberosities, approximately 1.5 mm. thick and ½ mm. high, whose walls are composed of a sclerenchymatous exterior and a thin inner peridium. At maturity, a yellow fascicle of sporogenous hyphae and capillitium breaks from the middle of the tuberosity. This fascicle towers like a column above the peridial crater. In contrast to the uninucleate cells of the vegetative hyphae, each of the cells of the sporogenous hyphae contains a dicaryon of unknown origin. These cells sprout laterally in basipetal sequence to three to six spore initials, divide into two daughter cells which round off and gradually, with the fusion of the dicaryon, develop to thick-walled smut spores (gemmae). In germination the diploid nucleus divides into four daughter nuclei, one of which remains in the smut spore while the other three migrate into the germ tube and become separated from each other by septa. Under favorable conditions of nourishment, the germ tube may sprout.

Shropshiria Chusqueae (Stevens, 1927) on *Chusquea simpliciflora* has been referred to this family by its author. In this genus the cups

are sunken in a sclerotium, with their tops and spore masses projecting slightly above the surface. Unfortunately the life cycle has not been studied.

In the Ustilaginales, three types of life cycles may be distinguished. The first type includes *Ustilago Zeae, Doassansia Sagittariae* and *Graphiola Phoenics;* it is related to the micro- forms of the Uredinales and to *Schizosaccharomyces octosporus* of the yeasts. The structure of the peridial walls of the Graphiolaceae also suggests a further development of the aecidium of a micro- form of the Uredinales. This type of life cycle is shown in the following diagram:

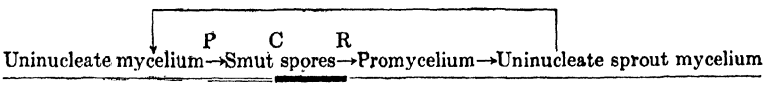


DIAGRAM XXXIX.

The second type includes *Ustilago violacea* and the majority of the smuts. It possesses no analog in the Uredinales; among the yeasts it corresponds to the *Saccharomycodes Ludwigii* type, *mutatis mutandis:*

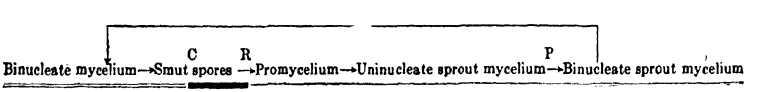


DIAGRAM XL.

The third type is only known in *Tuburcinia primulicola.* It also has no analog among the Uredinales:

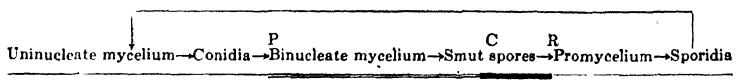


DIAGRAM XII.

Cytologically, the life cycle of the smuts is just as labile as that of the yeasts and rusts. As in these, species of the same genus behave entirely differently, *e.g.,* as *Ustilago Zeae* and *U. violacea* or *Doassansia Alismatis* and *D. Sagittariae, Tuburcinia Trientalis* and *T. primulicola.* Shiftings appear especially in end forms.

As in the above, the actual relationships of the Ustilaginales have been presented as objectively as possible; it will be attempted to interpret them briefly. The smut spores, which always caryologically function as zeugites, are the stable points in a multitude of forms; in this respect, and also biologically, they are homologous to the teliospores of the Ure-

dinales and have often been called teliospores. Whether they are homologous with them in the life cycle is still uncertain; in the forms of the type of *Entyloma Nymphaeae*, where they are formed terminally on small branches, this conception is plausible; for *Ustilago Tragopogonis-pratensis*, in which they arise from intercalary swellings, we possess no analog in the Uredinales. The only possible parallel at present are the chlamydospores of the Protomycetaceae. The smut spores of the Ustilaginales are also called chalamydospores. The chlamydospores of the Protomycetaceae germinate with sporangia with endogenous sporangiospores, while those of the Ustilaginales with basidia-like promycelia.

The morphological evaluation of this promycelium encounters great difficulties. Many older authors agree with Brefeld in considering it a conidiophore, or a hemibasidium which is in the process of stabilization to a basidium. The lowest stage was shown by *Ustilago longissima*, in which the sprout cells (considered by Brefeld as conidia) develop repeatedly to "conidiophores" of indefinite structure or to mycelia (*Pro-Ustilago*). A middle stage was shown by *U. Vaillantii* in which the "conidiophores" (sprout cells) could arise in unlimited sequence, but have become constant in form and septation (*Hemi-Ustilago*). The highest stage was shown by the type of *U. violacea*, in which the conidiophore was stabilized both in form and place of formation, appearing as a typical basidium only on the germination of the smut spores (*Eu-Ustilago*). According to this conception, then, the Ustilaginales should not be classed in the Basidiomycetes, but placed in a special class, the Hemibasidii, forming the transition from the Phycomycetes to the Basidiomycetes.

According to the point of view presented in this book, the state of affairs is quite the opposite. The promycelium of the Ustilaginales is not a hemibasidium (a basidium *in statu nascendi*) but a metabasidium (a basidium in degeneration). For this conception the following facts may be set forth: Already in the Uredinales some forms, *e.g.*, *Puccinia Malvacearum* (p. 581), have a tendency to omit the formation of basidiospores and to permit the basidial cells to germinate directly by germ tubes. This may be indicated as the first symptom of a development which, in respect to the morphological differentiation of the gonotoconts, proceeds in the reverse sense to that described for the transition from the Phycomycetes to the Ascomycetes. While in passing from the Phycomycetes to the Ascomycetes meiosis became fixed in a sporophore, the sporangium, which as gonotocont has developed to an ascus and finally to a basidium, thereafter, in the highest Basidiomycetes, the sporophore characteristic of these gonotoconts again begins to vanish. With the degeneration of sexuality, the gonotoconts also lose their typical form and again germinate directly to mycelia without spore formation as they did in the Phycomycetes. That these phenomena first appear in parasitic forms agrees

with the general experience that in these, the hereditary fixed characters are again set free.

In the Ustilaginaceae which in many respects, *e.g.*, in regard to parasitism in intercellular spaces, are more pronouncedly parasitic than the Uredinales but can also be saprophytic, one can explain on biological grounds the vegetative germination of the promycelium more simply than in *Puccinia Malvacearum*. In contrast to the Uredinales, on the germination of the smut spores there follows a longer saprophytic portion of existence (indicated by the sprout mycelium) which has so markedly characterized the majority of the species here considered that at this stage of development, only sprout mycelium is known. Thus, it is not surprising that this sprouting has displaced the formation of the now biologically superfluous basidiospores and proceeds directly from promycelium.

Thus we have in the Ustilaginaceae a last member of a phylogenetic series which includes *Platygloea* and *Septobasidium* in the Auriculariales, *Tremella* and *Sirobasidium* in the Tremellales and *Kordyana* and *Exobasidium* in the Cantharellales, where the basidiospores germinate chiefly or regularly by sprout mycelia. This would have the effect that not only the basidiospores, which in part remain on the basidium, develop to sprout mycelia but that the sprout mycelium, without this circuit, arises directly from the basidial cells. Here, apparently, we have the same phenomena which we were able to pursue step by step in the Endomycetaceae–Saccharomycetaceae series of the Ascomycetes where the asci no longer proceed to ascospore formation but germinate directly to sprout mycelia.

In the Saccharomycetes, the asci, because of their direct development to sprout mycelia, lost their characters of sporophores (sporangia) and became vegetative structures. In the Ustilaginaceae the basidia, by the elimination of basidiospore formation and vegetative germination, lost successively their characters as basidia; the division into four in the promycelium, having become senseless in the absence of spore formation, has disappeared and the germ tube which arises from the smut spores proceeds directly to the formation of sprout mycelium. It is perhaps no accident that the form most marked in this direction, *Ustilago longissima*, inhabits a waterplant, whereby the extreme development of the pellicle sprout mycelium may be explained as a biological adaptation. *U. longissima*, *U. bromivora*, etc., would be considered end forms in which the gonotocont has lost its typical form and was replaced by a purely vegetative germination. *Pro-Ustilago*, *Hemi-Ustilago* and *Eu-Ustilago* are therefore not a phylogenetically conditioned, ascending series but a biologically conditioned, descending series with constantly increasing intensity of adaptation which begins with *Eu-Ustilago* and in *Pro-Ustilago* disappears with complete obliteration of morphological characteristics.

This point of view which has been developed in regard to the Ustilaginaceae may be carried over directly to the Tilletiaceae. Here there can be no doubt that we have in the structures indicated as sporidia, the remains of basidiospores. Their survival lies in the fact that in the Tilletiaceae, in contrast to the Ustilaginaceae, the mycelial growth by sprouting has much receded or is entirely lacking, hence the reasons given above for the suppression of the basidiospores no longer hold. This original position of the Tilletiaceae is suggested by the fact that in them, *e.g.*, *Tilletia*, *Tuburcinia* and *Entyloma*, the mycelium still cuts off true conidia whereas these are absent in the Ustilaginaceae. On the other hand the basidia of the Tilletiaceae have lost the otherwise most characteristic points of basidia, the constancy of the spore number and the occurrence of the nuclear divisions in them. The nuclear divisions are, as in individual Ustilaginaceae, shifted forward into the smut spores so that in *Neovossia* the spore number may multiply. The next question is whether and how far these phenomena can be explained by biological influences. *Neovossia* suggests many Discomycetes in which the spore number is increased by the mitosis of the tetracyte nucleus.

In the mutual relationship of the Ustilaginaceae and Tilletiaceae, we rely as much on pure speculation as on the interpretation of the promycelia. Although the Ustilaginaceous basidium is undoubtedly connected to the Auricularia type, the terminal insertion of the sporidia on the Tilletiaceous basidium points to an autobasidium. Hence it is not impossible that both families, in spite of the similar structure of their spores and the tendency to the formation of spore balls, in biological relationship and pathological picture, represent two entirely distinct phylogenetic lines, markedly convergent because of their parisitism. When therefore we considered the Ustilaginales among the Phragmobasidiomycetes in connection with the Uredinales, this is only justified for the Ustilaginaceae while for the Tilletiaceae there are many possibilities.

The ancestry of the Ustilaginales is not to be sought in the highly specialized, parasitic, degenerate forms on gramineous hosts but in genera of the *Tuburcinia* type. Vuillemin (1897, 1905) suggests the Hypostomaceae whose two species, *Meria Laricis* and *Hypostomum Flichianum*, greatly resemble the Ustilaginaceae, but, owing to lack of cytological investigation, are not to be formulated in detail. Following this suggestion, let us consider *Septobasidium albidum*, comparing the conidial and basidial portions of its life cycle with the conidial and smut spore portion of the *Tuburcinia* type. The roots of the Ustilaginaceae would then (as those of the Uredinales with which they correspond in the strong, already fixed, shifting of their developmental rhythm, eu-, endo- and micro- type corresponding to *Ustilago Zeae* and *U. violacea*) be sought

in the Auriculariales, which is expressed provisionally in the following scheme:

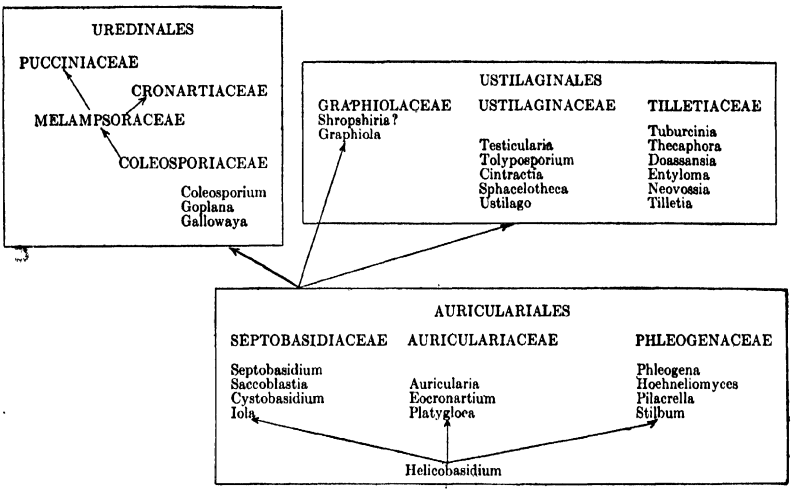


DIAGRAM XLII.

In regard to their life cycle, one should consider *Ustilago Zeae* and *Doassansia Sagittariae* as ancestral among the reduced forms and *Ustilago violacea* and *Tilletia Tritici*, further differentiated.

CHAPTER XXXV

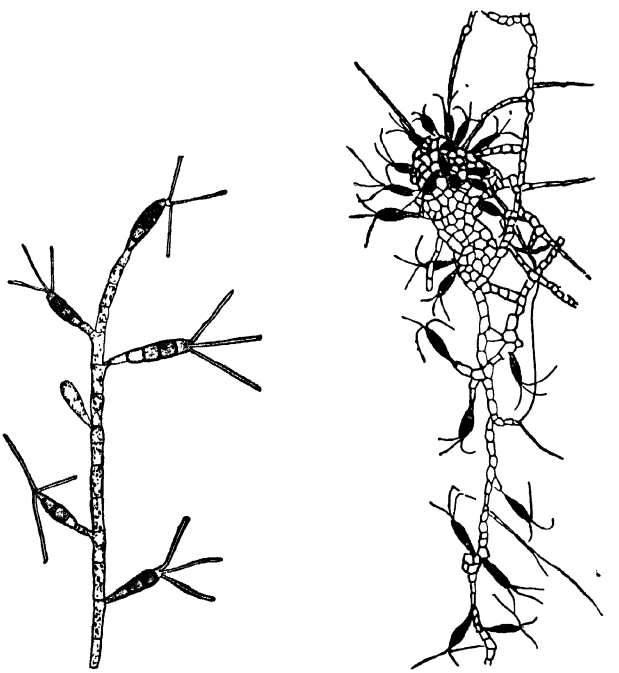
FUNGI IMPERFECTI

As the classification of fungi rests upon the life cycle of the individual species, of the various spore forms, only the asci and basidia, which in their character as *gonotocont*s play an important part in the cycle, are largely used as a means of classification. There is no place in this system for the imperfect forms which must be separately discussed until the group to which the life cycle belongs, has been discovered. In this connection, we may recall the *Oedocephalum* type which appears in the life cycle of the Mucoraceae in the Phycomycetes (Fig. 60) of the Pezizaceae in the Ascomycetes (Fig. 224), and of the Polyporaceae in the Basidiomycetes (Fig. 288). Since for practical purposes one must name and classify these imperfect forms somewhere, they have been grouped as Fungi Imperfecti (Fungi with incomplete or incompletely known life cycles). It is clear that in this group there can be no natural families and genera in the sense of phylogenetic unities, but only artificial groups of forms. Cytologically these imperfect forms are mostly haplonts; the only regular diploid imperfect form, the uredinium of the rusts, because of its characteristic structure immediately shows its systematic position.

The older classification of Fungi Imperfecti, developed by Saccardo in his *Sylloge Fungorum*, proposes three main groups: the Hyphomycetes, in which the conidiophores arise singly on mycelium, or, at most, are joined into coremia; the Melanconiales, in which they are formed on stromata (acervuli); and the Sphaeropsidales, in which they are inclosed in pycnia. Obviously this classification is only a makeshift and is encumbered with all sorts of misfits. For example, *Pestalotia versicolor* (*P. Palmarum*) forms solitary conidia on hyphae, in nutrient solution (Fig. 404, 2) and in this stage must be placed in the Hyphomycetes. Under more favorable conditions of nourishment, the hyphae intertwine to stromatic layers which may become pseudoparenchyma by the reciprocal, polyhedral flattening of the cells; the conidia arise either directly on this stroma or on single hyphae; occasionally the tissue arches over to a kind of pycnium, which, however, is still formed of hyphal tissue and is usually called **pseudopycnium.** In this stage, the fungus must be assigned to the Melanconiales. Finally, under certain conditions, one can obtain the type of fructification ordinarily seen in Nature, the pycnia; in this stage the fungus undoubtedly belongs to the Sphaeropsidales. Where we do not know the ontogenetic relations, a fungus may be placed in

different groups and named differently according to the stage of development. We have observed this earlier in the synonymy of the pathogenic Ascomycetes.

There is also the difficulty that all forms of conidial fructifications do not permit of arrangement in Saccardo's scheme (*e.g.*, *Leucophlebs*, Zeller and C. W. Dodge, 1924). Therefore there has been an attempt to enlarge the system or to replace it by a different one. Thus Potebnia



A *B*

FIG. 404.—*Pestalotia versicolor*. *A*. Conidia on branched hypha. *B*. Young stromatic layer formed in a solution. (*After Leiniger*, 1911.)

(1909) attempts to classify these fungi into five instead of three, groups: the Hyphales, in which the conidial hyphae are free; the Coremiales, in which they are united into coremia; the Acervulales, in which the conidia are borne on the upper surface of stromata; the Pseudopycnidiales, in which the conidia are borne in pseudopycnia, which either, as in the perithecia of the Plectascales, rupture irregularly or by narrow slits (Leptostromataceae type) or, as in the apothecia of the Discomycetes, become patelliform at maturity (Excipulaceae type); and into the Pycnidiales, in which the conidia are enclosed in true pycnia.

In another direction Höhnel (1923) attempts in a posthumous work to rearrange the entire system. He divides the Fungi Imperfecti into three groups: the Hyphomycetes, which correspond to Saccardo's group of the same name; the Synnematomycetes, which in the main include the Coremiales of Potebnia; and the Histiomycetes, to which belong collectively the forms with plectenchymatous stromata or fructifications (Acervulales, Pseudopycnidiales and Pycnidiales of Potebnia). The gigantic group of Histiomycetes he divides again into a large number of

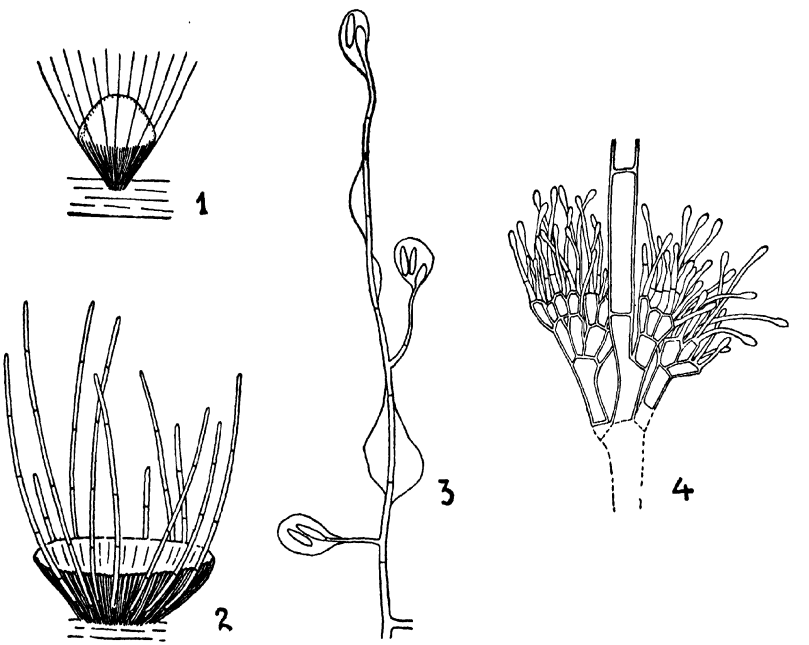


FIG. 405.—*Volutella scopula*. 1. Mature sporodochium. 2. Young sporodochium which has not started the production of conidia. 3. Conidia. A group of spores lie imbedded in a gel at the tips of the hyphae. 4. One of the large hyphae of the sporodochium and the conidiophores. (1 × 7; 2 × 30; 3, 4 × 780; *after Boulanger*, 1897.)

new groups, for name and definition of which one should turn to the original.

However much these forms may be justified in individual cases, one cannot avoid the impression that the Fungi Imperfecti are better off the less their classification is patched. It is of no great importance from which point of view they are regarded, since one only strives to catalogue them so that one may locate again a definite form with the least expenditure of energy. If one fundamentally changes the structure of this catalogue, confusion results which can be of no profit to the catalogue

or its user. In this sense, it appears that Saccardo's system, as expanded by Lindau (1900, 1907–1910), by Allescher (1901–1903) and by Diedicke (1915), serves all practical purposes.

In Saccardo's system, the Hyphomycetes are classified in four subgroups: in the Mucedineae and Dematieae the hyphae and conidiophores are always solitary, in the first, hyaline or brightly colored, in the latter, brown or black; in the Stilbeae the hyphae are united into coremia, and in the Tuberculariеae to pulvinate stromata. Each of these suborders is divided by spore characters: spores unicellular, Amerosporeae, *e.g.*, in the Mucedineae, *Aspergillus* (Fig. 110), *Penicillium* (Fig. 6), *Monilia* (Fig. 213) and *Botrytis* (Fig. 215); in the Dematieae, *Thielaviopsis* (conidia like *Thielavia*, Fig. 108); in the Stilbeae, *Isaria* (Fig. 167); in the Tuberculariеae, *Volutella* (Fig. 405). Spores two-celled: Didymosporeae (*e.g.*, *Cladosporium*); spores three or more celled: Phragmosporeae (*e.g.*, *Fusarium*, etc.). According to need in each of these groups, the hyaline and colored spore forms may be separated into special series, *e.g.*, the Amerosporeae into the Hyalosporeae and the Phaeosporeae, and the Didymoporeae into the Hyalodidymeae and Phaeodidymeae, etc.

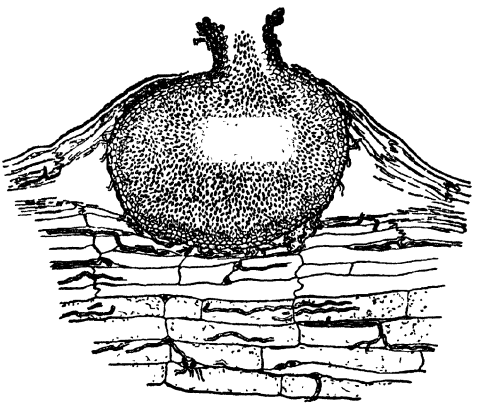


FIG. 406.—*Phoma apiicola.* Pycnium on a root of celery. (*After Klebahn.*)

A similar classification may be made for the Melanconiales; *e.g.*, there are among the Melanconial Hyalosporeae, *Sphacelia* (Fig. 162, *D*) *Gloeosporium* (Fig. 183, *b*) and *Collectotrichum*, and in the Hyalodidymeae, *Marssonina.*

In the Sphaeropsidales, four subgroups are first distinguished: the Sphaerioideae with black, membranous pycnia; the Nectrioideae with light-colored, fleshy pycnia; and the Leptostromataceae and Excipulaceae whose characteristics have been given above. The Hyalosporeae of the Sphaerioideae contain the *Phyllosticta–Phoma* group (Fig. 406); the Phaeosporeae, *Coniothyrium;* the Hyalodidymeae, *Ascochyta;* the Scolecosporeae (spores multicellular, slender), *Septoria* (Fig. 8), and in the Excipulaceae, *Discula* (Fig. 183, *d*) is an example of the Hyalosporeae.

Naturally it would be desirable to have the Fungi Imperfecti entirely disappear as a group, and be distributed among the natural orders of fungi. It will be generations, however, before this hope will be realized.

CHAPTER XXXVI

REVIEW OF FUNGOUS CLASSIFICATION

In the fullness of the problems and the ontogenetic peculiarities encountered in the forgoing treatment, the general aspects may have been somewhat obscured. Hence in conclusion we give a brief review of the important lines as they appear to the author.

The twenty-seven orders of fungi discussed in this book are united in a two-dimensional diagram into a phylogenetic scheme of their probable more important morphological relationships. From the Flagellates–Myxomycetes may have arisen the heterogeneous class of the Archimy-

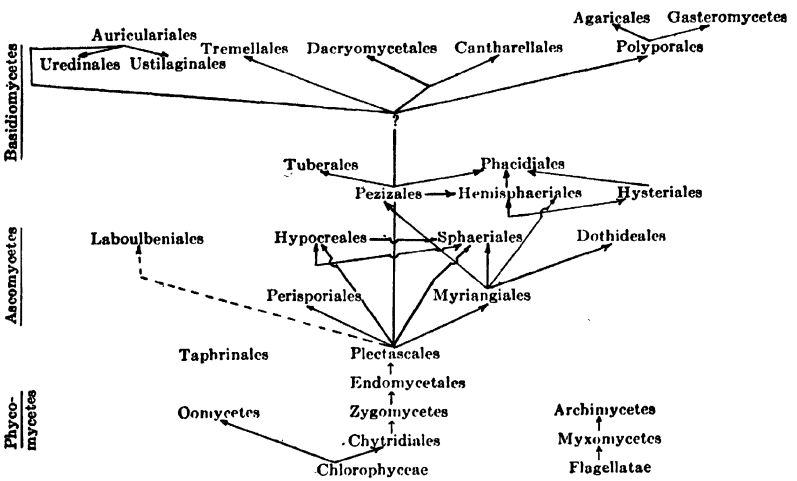


DIAGRAM XLIII.

cetes (p. 17) whose representatives, probably only on historical grounds because of their parasitism on plants, found a refuge in the fungi to which they are otherwise entirely foreign.

All true fungi are derived from green algae in monophyletic line. They first divide into two series: an oogamous, the Oomycetes (p. 54), and a zygogamous, the Chytridiales–Zygomycetes (pp. 33 and 92) which, both in their imperfect forms and in the behavior of their gametangia, undergo similar stages of degeneration.

A. Imperfect Forms.—The individualization of daughter cells of sporangia (the zoospores in the Oomycetes and many Chytridiales and

the sporangiospores of certain Zygomycetes) is retarded and the sporangia germinate with germ tubes before this individualization has begun; consequently they gradually assume the function of their daughter cells, especially that of propagation, and gradually separate as a whole from the mother plant and become conidia (p. 30). In the Oomycetes, this reduction of the sporangium to a single spore occurs exclusively by an inhibition of zoospore formation; thus it has remained an entirely internal process which has not had direct reaction on the form and size of sporangia (pp. 74–78). In the Zygomycetes discussed here (pp. 104–108), however, the primary consideration is not in the inhibition of the formation of sporangiospores whose individuality is retained, but in the degeneration of sporangia; to a certain degree the pressure comes from the outside and with the decrease in size of sporangia leads also to a decrease in number of sporangiospores; in place of many-spored sporangia, there arises a single conidium. Thus in the oogamous and zygogamous series the releasing forces have been of a different nature but the effect has been the same: the functions of the daughter cells are gradually assumed by the mother cells; this is the indication of degeneration: *totum pro parte*. Besides in the *Choanephora–Piptocephalis* series of the Zygomycetes (pp. 101–105), we have an example of how, by retardation of spore formation, the spores can be formed exogenously instead of endogenously and how, consequently, a form of fructification can divide into two types whose genetic connection may only be determined experimentally.

B. Gametangia.—As in the sporangia, so also in the gametangia, which have apparently arisen from sporangia, there is no individualization of single energids and instead of two true uninucleate gametes, so-called merogamy, there appears first the copulation of (coenocytic) gametangia themselves (p. 59 *et seq.*). As the sporangia, so also the gametangia assume the functions of their daughter cells; again *totum pro parte* instead of *pars pro toto*, the indication of genetic degeneration.

With this deuterogamous substitute of the original merogamy begins that crisis of sexuality that may be traced through the whole system of fungi. At first it would seem as if these membrane-surrounded gametangia offered a definite biological advantage over the naked gametes, for it is no longer left to chance whether two gametes find each other, but the gametangia themselves provide that the nuclei of both parents should reach each other and become sexually active. Thus fewer sexual cells are formed but they are better developed. Furthermore, this development from merogamy to gametangial copulation (parallel with the development of imperfect forms from hydrochory to anemochory) has made possible or facilitated the transition of fungi from aquatic to terrestrial habitats and to parasitism in the interior of other plants (p. 73 *et seq.*). Thus at first the gametangia functioning as sexual cells undoubtedly show a further development; this may be observed both in the oogamous and

zygogamous series, but the details in both series differ characteristically. We will review only two points, important for the course of the discussion.

A first point lies in the striving for a uninucleate condition of the sexual cells, by which the development of uninucleate gametes to multinucleate (polyenergid) gametangia (so-called coenogametes) is again paralyzed. In the Oomycetes this tendency expresses itself next (in the Saprolegniaceae p. 68) in the female gametangia by the degeneration of a portion of the nuclei before and during their activation as sexual nuclei, wherefore the content of the gametangia round up about the remaining, privileged sexual nuclei, forming egg cells. Thus the virtually female gametes within the coenocytic gametangia recover functionally their earlier individuality; they no longer swarm but each secures for itself a male nucleus by means of a special branch of the reproductive sac. In the Peronosporaceae, the differentiation between the functional and supernumerary female energids (or sexual nuclei) extends to the protoplasm, and separates it as gonoplasm which is used for the fundaments of the single eggs, and periplasm which serves only vegetative purposes. Thereupon selection goes still further and moves all but one of the privileged sexual nuclei from the coenocytic egg cell into the periplasm, where they function vegetatively (pp. 80–87). In the Zygomycetes this tendency expresses itself by a lessening of the number of active sexual nuclei so that in *Endogone lactiflua* (p. 115) all but the one functional nucleus at the base of the copulation branch withdraw and are abjointed from the gametangium proper. With the privileging of a single sexual nucleus, the oogamous and zygogamous series have again reached the stage of the lowest fungi as regards the effect of their sexual organs: again a single uninucleate zygote, arises as the product of the sexual act; only this uninucleate zygote, which in *Olpidium* and *Monoblepharis* was the product of two daughter cells of the gametangia, is now the product of two gametangia themselves: as in the retrogression of the sporangia to conidia, here too the whole organ assumes the function of its part.

A second point in the development of gametangia lies in the retardation of caryogamy; this no longer immediately follows on the completion of the sexual act, plasmogamy, but it may be postponed for months in both the oogamous and zygogamous series (pp. 84, 112); in certain forms, as in *Basidiobolus* (p. 118), its initiation is dependent upon environment, and is hastened by drying out and retarded by liberal nourishment. This retardation of caryogamy is accompanied in the higher forms by a shifting in position: the zygote continues its growth before the occurrence of caryogamy in the outgrowths of the zygotes (*e.g.*, in *Endogone*, p. 115). Similarly, meiosis may be retarded and shifted, so that it occurs only in the sporangia which arise on the germination of the zygotes (*e.g.*, in the "germ sporangia" of *Phycomyces*, (p. 112).

According to the theory here expressed, the Ascomycetes will connect to the Phycomycetes and particularly to hypothetical Zygomycetes of the *Endogone* type, in which there arises directly, as the product of the sexual act, a sporangium (the ascus) instead of a zygospore germinating with a sporangium. While in the Phycomycetes, the sexual act leads first to the formation of a resting spore, in the lowest Ascomycetes, the Hemiasci (p. 137), it leads directly to propagation. These lowest Ascomycetes still possess in part, like *Endogone*, polyenergid gametangia in which each nucleus is privileged as active sexual nucleus (*e.g.*, *Dipodascus*, p. 137; *Endomyces Magnusii*, p. 143). While in *Endomyces Magnusii*, as in *Endogone*, the supernumerary nuclei migrate downwards, in *Dipodascus* they remain in the mature gametangia beside the functional sexual nuclei; here they persist and at maturation of the zygotes serve vegetative purposes.

This circumstance, that in the young germ sporangia of *Dipodascus* (*i.e.*, in the young asci) numerous sporogenous gametangial nuclei are present, besides the daughter nuclei of the diploid fusion nucleus which are capable of spore formation, is strikingly reminiscent of the relationships just described for the phylogeny of the Oomycetes. In the Saprolegniaceae, even at the time of egg formation, the supernumerary gametangial nuclei have already degenerated, so that (*mutatis mutandis* as in the sporangia of the Zygomycetes) the whole content of the female gametangium more or less cleaves into oospheres (p. 67). The case is similar for *Phytophthora* (p. 82). In the higher species of *Peronospora* and in some of *Albugo* (p. 84, *et seq.*), a portion of the supernumerary nuclei remains at the periphery of the female gametangium, so that the contents of this gametangium separate as a central egg cell, which serves the true sexual function, and into a peripheral periplasm that performs only vegetative tasks. A convergent development has apparently occurred in the Zygomycetous sporangia which have become gonotoconts. If the contents of these sporangia divide directly by cleavage, as occurs in the ordinary sporangia of the Zygomycetes, the remaining, non-privileged, gametangial nuclei would pass into the spores; that can only be avoided if each of the sporogenous nuclei forms a membrane in its environs which leaves unused as (vegetative) periplasm the remaining protoplasm and the gametangial nuclei. In this sense, the ascus of the Ascomycetes and the oogonium of the Oomycetes may be regarded as analogous structures.

One must, then, apparently imagine that the sporangia of the here discussed (hypothetical) Zygomycetes have split into two types, just as occurred in another direction in the *Choanephora–Blakeslea* group (pp. 100–105). The ordinary vegetative sporangia retained their Zygomycetous character (division into spores by cleavage) and developed gradually to exogenous forms (*Cunninghamella–Syncephalis–Aspergillus* group);

the germ sporangia which have become gonotoconts, however, at first retained their endogenous spore formation but later, because of the long life of the non-privileged sexual nuclei, passed from cleavage to free cell formation and became asci. Thus the ascus would be a Zygomycetous sporangium which, in its character as gonotocont, has become constant in form and spore number.

According to this conception, then, the step from the Zygomycetes to the Hemiasci would consist in the differentiation of the germ sporangium to an ascus conditioned by the privileging of sexual nuclei, while the structure of the sexual organs themselves and the place of caryogamy remains unaltered. In the step from Hemiasci to Euascomycetes (p.166) the second point raised for the Phycomycetes, the retardation of caryogamy becomes morphologically operative. For some reason caryogamy is more retarded than in *Endogone* (an intermediate form is not known, with the exception of a suggestion of one in *Endomyces Lindneri* (p. 142) so that the zygotes not only, as in *Endogone*, develop to unicellular dicaryotic appendages, but by repeated division of the nuclear pair also develop to much-branched dicaryotic hyphae, the ascogenous hyphae. As fertilization remains fixed in the asci, which therefore serve simultaneously as zeugites and gonotoconts, plasmogamy and caryogamy are separated in time and space by this insertion of ascogenous hyphae; reproduction is separated in time and space from the sexual act causing it.

Thus in the life cycle of the Euascomycetes we find a new section, the dicaryophase, whose soma, at first physiologically independent, is embedded in the haplont and nourished by it, and in the most extreme case (in *Penicillium crustaceum*, p. 184) loses its organic connection with the haplont and is parasitic on it. These dicaryotic hyphae in their various types (p. 129) present numerous morphological problems; they may be interpreted as an attempt at a diploid stage which was not possible in this lowest developmental stage of organic life, but which found a physiological, though not morphological, solution in the formation of dicaryons.

By these multiple, ramose, ascogenous hyphae a whole series of ontogenetic possibilities is suddenly opened to the Euascomycetes; the degree of activity of their gametangia increases in geometric progression, so that, even when the gametangia are uninucleate, several fertilizations are accomplished by one plasmogamy (*e.g.*, *Polystigma rubrum*, p. 229, in contrast to *Eremascus fertilis*, p. 139). Similarly, all dicaryons in the polyenergid gametangium retain full activity. The multiple dicaryons of the *Pyronema* type (p. 332), in contrast to the multiple dicaryons of *Albugo Bliti* and *A. Portulacae*, are followed by a corresponding increase in the number of gonotoconts, hence it seems to be significant that in these higher Ascomycetes, the principle of the privileging of a few sexual nuclei may no longer be demonstrated.

As a consequence of this numerical increase, the asci of the Euascomycetes gradually acquire the significance of new integral forms of fructification, which finally become so predominant that they are called the perfect forms. The life cycle of the Euascomycetes, consequently, divides into two cycles whose rhythms run parallel or in sequence; into an asexual cycle in the haplont propagating by imperfect forms, conidia, *etc.*, and into a sexual cycle which occurs in the dicaryophase and concludes with the perfect form, the asci. In the lower Euascomycetes, *e.g.*, in the lower Plectascales, (p. 166) the asexual cycle predominates; in the highest Euascomycetes, *e.g.*, in the Helvellaceae (p. 346) and the Tuberales (p. 354), the sexual cycle predominates. Between these groups in which both rhythms have developed equally and lead to fructifications standing morphologically at the same height, as the Nectriaceae, *Tuberculariа*, fructification of imperfect form; *Nectria* stromata, fructification of perfect form (p. 236); the *Polystigma* group, pycnia, fructification of imperfect form, perithecia, fructifications of perfect form (p. 229) and the *Cordyceps* group, *Isaria*, fructification of imperfect form, *Cordyceps* stromata, fructifications of perfect forms (p. 253).

Differing from this rapid ascent of the Euascomycetes in regard to their fructification, especially those of the perfect form, they show astonishing identity of sexual organs. Even in the lowest forms the archicarps undergo a further differentiation into a receptive organ, the trichogyne, and the true functional part the ascogonium (*Monascus–Pyronema* type), both of which types are subsequently repeatedly septate and coil; this development, however, is notably limited to the female gametangia as in the fungi altogether only these (as their various names, oogonium, ascogonium, scolecite, *etc.*, indicate) have undergone a further morphological development. For the rest the condition caused by this functional differentiation is retained in entire uniformity throughout all twelve orders of the Euascomycetes as, to cite a few of the more important forms studied cytologically, the *Gymnoascus–Monascus–Magnusia* group of the Plectascales (p. 166) and the *Erysiphe–Sphaerotheca–Phyllactinia–Lanomyces* group of the Perisporiales (p. 192), in *Claviceps purpurea* of the Hypocreales (p. 248), *Venturia inaequalis* of the Sphaeriales (p. 269), *Stigmatea Robertiani* of the Hemisphaeriales (p. 298), *Cryptomyces Pteridis* of the Phacidiales (p. 308) and in the Pezizales, in *Pyronema confluens*, *Ascodesmis nigricans*, *Ascobolus vinosus*, *Lasiobolus brachyascus* etc. (p. 332).

Besides this apparent constancy may be noted a peculiar degeneration of sexuality which first appears in a functional degeneration of the antheridium. In some forms, as in the *Pyronema confluens–Ascodesmis nigricans* group (pp. 332–336), they have become entirely facultative and dependent on nutritive conditions; in other forms, as *Lachnea stercorea* (p. 343), they still fuse with the ascogonia but nuclear migration

no longer occurs; in still other forms, as the *Amauroascus–Ctenomyces–Aphanoascus* group of the Plectascales and in *Pyronema confluens*, var. *inigneum* of the Pezizales (p. 169 and 335), they no longer fuse with the ascogonia; at least in *Pyronema confluens*, var. *inigneum*, however, they coil about the trichogyne several times and finally, in forms such as *Penicillium vermiculatum* (p. 180), they are retarded and are only ready to function when the ascogonia have passed capability of fertilization. In all these cases the nuclei in the ascogonium pair autogamously and continue to develop as if copulation had occurred.

In the direct relations of all these forms a morphological as well as a functional weakness of the antheridia develops; the functionless antheridia are eventually no longer formed and the ascogonia are solitary, as in the *Aspergillus herbariorum–A. flavus* series of the Plectascales (p. 182), in the *Melanospora–Neurospora* series of the Hypocreales (p. 226), in the *Chaetomium globosum–C. spirale* series of the Sphaeriales (p. 257), in the *Ascobolus magnificus–A. citrinus* series of the Ascobolaceae (p. 338) and in the *Lachnea scutellata–L. stercorea* series of the Pezizaceae (p. 343) in the Pezizales. That this morphological degeneration is similar in very different orders allows one to assume a fundamental law.

As compensation for this lack of organic cross fertilization by the degeneration of the antheridium, two groups of substitute functions appear subsequently one of which is reminiscent of the earlier cross fertilization, while the other leads directly to autogamy.

In the first group, to which belong *Ascobolus carbonarius* of the Pezizales (p. 340) and *Collema pulposum* and *C. crispum* of the Discomycetous lichens (p. 350), the trichogynes, for lack of antheridia, copulate with imperfect forms, conidia and oidia. To explain these relationships, one may assume, in consideration of the relationships of the Basidiomycetes, that some of these forms are heterothallic; although the male mycelium by the loss of antheridia has morphologically become imperfect, they retained (as the later pseudogamous types show) their sexual character, so that thereafter the imperfect forms in place of the only slightly differentiated antheridia assume the function of male sexual cells. In the homothallic forms, one must imagine that the ascogonia, for some reason or other, possess a stronger affinity to these imperfect forms than to the usual mycelial cells.

This conidial copulation actually causes great difficulties in the monophyletic derivation of fungi proposed in this book and other equally unsatisfactory explanations are offered. Thus Dangeard considers that in primitive gametangia, *e.g.*, of the *Monoblepharis* type, the male gametes lost their motility and became male akinetes which might have appeared similar to the sporangiospores of the Mucoraceae. Just as these sporangiospores of the Mucoraceae gradually developed exo-

spores, so that the sporangiophores became conidiophores, these male akinetes would have also developed to exospores and the male gametangia would then have become gametophores (in the Pezizales, Laboulbeniales, etc.). As plausible as this theory is, it breaks down from the entire absence of the hypothetic intermediate members. It is further difficult to explain why some male gametangia would have undergone such entirely different developments than other male and female gametangia.

In the second group mentioned above, which leads to autogamy, a parthenogamous sexual act first appears in the place of organic cross fertilization between two or more cells in the ascogonium; the septa are dissolved, the nuclei pair and migrate out into the ascogenous hyphae; to this parthenogamous type belong *Polystigma rubrum* (p. 229) in the Hypocreales, *Systremma Ulmi* (p. 291) in the Dothideales, *Rhytisma acerinum* (p. 312) of the Phacidiales, the *Leotia–Spathularia* group (p. 327) of the Geoglossaceae, *Rhizina undulata* of the Rhizinaceae, the *Ascobolus citrinus–Ascophanus carneus* group (p. 341) of the Ascobolaceae, the *Lachnea scutella–L. abundans* group of the Pezizaceae and the *Laboulbenia chaetophora–Laboulbenia Gyrinidarum* group of the Laboulbeniales. Thus the parthenogamous cell fusion is replaced by an autogamous nuclear pairing in the interior of one or more cells of the ascogonium, as in the *Ascophanus ochraceus–Saccobolus violascens* group of the Ascobolaceae (p. 342) and *Humaria granulata* of the Pezizaceae (p. 344). Hand in hand with all these functional degenerations, the archicarps lose their specific form, trichogyne, etc., and morphologically appear increasingly like the vegetative hyphae, as in the *Leotia–Spathularia* series of the Geoglossaceae, in *Lachnea abundans* and *Humaria rutilans* of the Pezizaceae and in the *Icmadophila–Baeomyces* series of the Discomycetous lichens. And, finally, this detour around the reduced female sexual organs disappears and the sexual acts no longer occur in special organs, but between ordinary vegetative hyphae, so that the ascogenous hyphae arise directly from vegetative hyphae rich in reserves, *e.g.*, in *Trichoglossum hirsutum* (p. 327) of the Geoglossaceae, *Humaria rutilans* of the Pezizaceae and *Baeomyces roseus* of the Discomycetous lichens.

Thus it is characteristic in the sexuality of the Euascomycetes that always different substitutes for the sexual act occur. If already in the Phycomycetes the gametangia replaced gametes, so in the Euascomycetes the male gametangia disappear, and the sexual act occurs between female gametangia and imperfect forms or in the interior of the female gametangia, between two or more sexual cells or in the interior of a single sexual cell, by simple nuclear pairing or, after the female gametangia have degenerated, without sexual organs between any two vegetative hyphae.

In both these partial processes, which together constitute copulation, plasmogamy and caryogamy, a shifting then a degeneration occurred.

Caryogamy and meiosis remain constant, however, in form and place. Correspondingly, the gonotoconts, the asci, show a remarkable stability in the mobile series of sexual organs and fructifications. After the Hemiascomycetes, where they have been stabilized to a definite form and spore number, they alone further undergo a development and secondary modifications in function (p. 135) but remain entirely the same in morphological features. The fact that this biological differentiation of the asci is retained while the imperfect forms are wanting, causes the position of the asci as perfect forms to appear more strongly; one has the impression that more weight would be placed on a suitable dissemination of ascospores (as the products of fertilization) than on the dissemination of conidial forms.

It appears, however, that the same laws which in the *Choanephora Blakeslea* group (pp. 101–102) retarded spore formation and shifted it to the exterior of the sporangia, must have gradually become active in the sporangia, the asci, which have become gonotoconts: in the *Cunninghamella–Syncephalis–Aspergillaceae* series, spore formation is shifted from the interior of the sporangia to their surface so that the sporangiophores became conidiophores. In time the asci also shifted their spore formation to the surface and thus became changed from sporangia to conidiophores (at first eight spores), to basidia. The basidium thus would be an ascus with exogenous spore formation. The usual Zygomycetous sporangia and the sporangia which have become gonotoconts (asci) would have gone through the same development from endogenous to exogenous spore formation; only in the usual sporangia this development occurred in a short span of time (genetically considered) while the sporangia which have become gonotoconts, because of their greater stability, became active much later. Apparently in this manner the lower Basidiomycetes have arisen from forms like *Ascocorticium* in the lower Ascomycetes.

The life cycle of these lower Basidiomycetes agrees entirely with that of the Euascomycetes. On the germination of their tetracytes, there first arises a haploid thallus whose structure appears entirely like that of the Euascomycetes and which propagates by imperfect forms fundamentally the same as those of the Euascomycetes (p. 397). Subsequently pseudogamous plasmogamy, occurring between its hyphae (as between the hyphae of the Euascomycetes), produces new dicaryotic hyphae; in both the Euascomycetes and the Basidiomycetes, sexual organs are suppressed and as evidence of earlier sexuality, there is only retained the dynamic differentiation of the mycelia into + and − strains (heterothallism). This dynamic differentiation, however, begins to lose its obligatory character and instead of the original antithetic (bipolar) sexual differentiation, there appears the multipolar (p. 399) which rests only on comparatively labile and dynamic gradations.

Besides in the Basidiomycetes, manifold morphological modifications occur in the pseudogamous sexual process; in parasitic forms (the Uredinales and some Ustilaginales) the plasmogamy is localized mainly in hyphal knots from which subsequently arise definite spore forms (aeciospores, p. 555; urediniospores, p. 564; and teliospores, p. 569. On the other hand, it may become entirely labile and, as sexual maturity apparently appears earlier and earlier, they move to the germ mycelia of the basidiospores, by increasing shortening of the haplont (*Peniophora Sambuci*, p. 400), and finally to the basidiospores (*Tilletia Tritici*, p. 596). Thus plasmogamy has become shifting, perittogamous. It seems as if it no longer mattered to the Basidiomycetes, as to the fungi in general, when, where and how plasmogamy occurs, so long as the double chromosome number is retained; the sporophytes are capable of greater morphological differentiation, however, than the gametophytes. Finally, also the indirect copulation of two basidiospores (which in any case is only a formality) disappears and the nucleus which has migrated into basidiospore (possibly like the original homothallic forms) divides directly into two daughter nuclei which henceforth behave as a dicaryon (*Gasteromycetous* type, p. 397). In this last stage of sexual degeneration, no foreign nuclear material is introduced from without and cytological development is wholly internal and intracellular (endocaryogamy in the stricter sense, in contrast to exocaryogamy). The *Corticium bombycinum* type no longer has plasmogamy but only caryogamy. The importance of this endocaryogamy, however, lies in the fact that it makes possible for the individuals in question synapsis and meiosis and consequently a new combination of their chromosomes, a relationship which, because it must lead to a cessation of phylogenetic development, undoubtedly suffices for the individual but not for the species. Hence the step to complete apogamy is short.

With this shifting of plasmogamy in space and time, there goes a degeneration as regards its content. Just as plasmogamy disappears and finally takes place only as an episodical occurrence between two vegetative hyphae somewhere outside in the mycelium, so also its products lose their specific character: the physiologically dependent, dicaryotic, ascogenous hyphae have become a secondary Basidiomycetous mycelium (p. 401), which henceforth, like any vegetative hyphae, is capable of independent existence, especially food intake (p. 405) and propagation by independent forms (p. 407) and, after its formation, develops with such complete habitual correspondence with the original haploid hyphae that, except for eventual clamp formation, its diploid character can only be definitely determined by cytological investigation. The difference between the Euascomycetes and Basidiomycetes in respect to their dicaryotic generation, is thus only quantitative; while in the Euascomycetes the haplont and diplont were two phases of a cycle, the second of

which was nourished by the first, in the Basidiomycetes they are two independent entities which, under certain conditions, both can propagate through imperfect forms and, *e.g.*, in the heteroecious rusts, differ characteristically in their physiological needs (p. 462). Thus in the Basidiomycetes, there has arisen between plasmogamy and caryogamy, a new independent entity, the dicaryophyte.

Corresponding to its newly acquired independence, this new dicaryophyte proceeds to the independent formation of fructifications (p. 407). These arise without the direct intervention of plasmogamy directly from physiological stimulation (p. 407) and thus, like the fructifications of the imperfect forms, are vegetative in origin (in contrast to the perithecia of the Plectascales and the Pyrenomycetes and the apothecia of certain Discomycetes); hercin exists the inherent contradiction in the phylogeny of the fungi: decline in sexuality and ascent in structure of the fructifications, is its natural solution. While in the Ascomycetes fructifications belonged to the haplophase and only bore the diplont as a dependent structure on or in them, in the Basidiomycetes, they belong entirely in the dicaryophase; thus in this respect, the scale Zygomycetes–Ascomycetes–Basidiomycetes corresponds to the Chlorophyceae–Bryophyta–Cormophyta series of the chlorophyllous plants. As the mechanical principles and structural materials, the hyphae are everywhere the same, the fructifications of Basidiomycetes (with the exception of the end forms in the Gasteromycetes) resemble both perfect and imperfect forms of the Ascomycetes (except for individualities which are determined by type of spore dissemination, p. 416) just as in the various series the Basidiomycetes have developed strongly converging types. Thus we find in both classes, the development from gymnocarpy to hemiangiocarpy and to hypogaeous forms. Similarly, to cite one example, the *Clavaria* type has been realized both in perfect and imperfect forms of Ascomycetes as well as in different series of Basidiomycetes. Only the fructifications of the Basidiomycetes, by a greater mass, effect an enormous waste of food.

Just as plasmogamy disappeared in the Basidiomycetes and its direct product, the dicaryophyte, lost its specific character, so thereafter the organs and products of caryogamy, the gonotoconts and tetracytes, begin to disappear. First they lose the gonotoconts, the basidia, which are a fixed form of asci, become plastic and varied (p. 413). Then, with the predominance of endocaryogamy, they acquire more and more the character of imperfect forms; thus in the Gasteromycetes, they lose their biologically unique position (p. 417) and differ only in internal cytological characters from conidial formations: in proportion as the asexual fructifications are lost the sexual fructification begins to become asexual. And, in a third direction, in both subclasses of the Basidiomycetes, as occurred already with plasmogamy and caryogamy in the transition from

Hemiascomycetes to Euascomycetes, caryogamy and meiosis are separated in time and space into two steps of division; caryogamy takes place in special organs, the zeugites, while only meiosis is retained in the basidia (Uredinales, pp. 562, 572 and 592; Ustilaginales, p. 599; Brachybasidiaceae, p. 433). While the zeugites undergo an increasingly richer development, septate and develop to independent spore forms, in the basidia, which only serve for meiosis, the basidial character becomes still weaker, as happened in the endocaryogamous forms: the obsolete rust basidia (type of *Puccinia Malvacearum*, p. 585) and the obsolete smut basidia (p. 585) begin as metabasidia to die away in purely vegetative germinations. In this manner, in the highest Basidiomycetes we descend again to the starting point of the Phycomycetes (p. 610).

BIBLIOGRAPHY

ADAMS, J. F., 1918, Origin and development of the lamellae in Schizophyllum, *Mem. Torrey Botan. Club*, **17**: 326–333, *pl. 9.*

———, 1919, Sexual fusions and development of the sexual organs in the Peridermiums, *Pennsylvania State College Agr. Exp. Sta. Bull.*, **160**: 31–76.

———, 1921, Gametophytic development of blister rusts, *Botan. Gaz.*, **71**: 131–137.

ADERHOLD, R., 1896, Die Fusicladien unserer Obstbäume, *Landw. Jahrb.*, **25**: 875–914.

———, 1900, Mycosphaerella cerasella n. spec. die Perithecienform von Cercospora cerasella Sacc. und ihre Entwicklung, *Ber. Deutsch. Botan. Ges.*, **18**: 246–249.

ADERHOLD, R., and W. RUHLAND, 1905, Zur Kenntnis der Obstbaumsklerotinien, *Arb. Biol. Reichsanst. Land-Forstw.*, **4**: 427–442, *pl. 7.*

ALLEN, C. A., 1906, The development of some species of Hypholoma, *Ann. Myc.*, **4**: 387–394, *pl. 5–7.*

ALLESCHER, A., 1901–1903, Fungi imperfecti in Rabenhorst, *Krypt. fl. Deutschl. Oesterr. u. d. Schweiz I*, **6**: 1–1016; **7**: 1–1072.

AMES, A., 1913, A consideration of structure in relation to genera of the Polyporaceae, *Ann. Myc.*, **11**: 211–253, *pl. 10–13.*

ANDERSON, P. J., 1913, Morphology and life history of the chestnut blight fungus, *Comm. Invest. Control Chestnut Blight Dis. Pennsylvania, Bull. 7.*

APPEL, O., and H. W. WOLLENWEBER, 1910, Grundlagen einer Monographie der Gattung Fusarium, *Arb. Biol. Reichsanst. Land-Forstw.*, **8**: 1–207.

ARNAUD, G., 1910, Contribution à l'étude des fumagines, *Ann. Myc.*, **8**: 470–476.

———, 1910, Contributions à l'étude des fumagines I, *Ann. École Nat. d'Agr. Montpellier*, 2 *sér.*, **9**: 239–288.

———, 1911, Contributions à l'étude des fumagines II, *Ann. École Nat. d'Agr. Montpellier*, 2 *sér.*, **10**: 211–330.

———, 1912, Contributions à l'étude des fumagines III, *Ann. École Nat. d'Agr. Montpellier*, 2 *sér.*, **12**: 1–34.

———, 1918, Les Asterinées, *Thèse* [Paris], 288 p.

———, 1921, Études sur les champignons parasites, *Ann. des Épiphyties*, **7**: 1–115, *pl. 1–10.*

———, 1923, Études sur les champignons parasites, *Ann. des Épiphyties*, **9**: 1–40.

ARTHUR, J. C., 1917, Orange rusts of Rubus, *Botan. Gaz.*, **63**: 501–515.

ATANASOFF, D., 1919, A novel method of ascospore discharge, *Mycologia*, **11**: 125–128.

ATKINSON, G. F., 1894, Artificial cultures of an entomogenous fungus, *Botan. Gaz.*, **19**: 129–135, *pl. 14–16.*

———, 1903, The genus Harpochytrium in the United States, *Ann. Myc.*, **1**: 479–502, *pl. 10.*

———, 1905, The genera Balansia and Dothichloe in the United States with a consideration of their economic importance, *Jour. Myc.*, **11**: 248–267, *pl. 81–88.*

———, 1905, Life history of Hypocrea alutacea, *Botan. Gaz.*, **40**: 401–417, *pl. 14–16.*

———, 1906, The development of Agaricus campestris, *Botan. Gaz.*, **42**: 241–264, *pl. 7–12.*

———, 1909, Some fungous parasites of algae, *Botan. Gaz.*, **48**: 321–338.

———, 1909*a*, Some problems in the evolution of the lower fungi, *Ann. Myc.*, **7**: 441–472.

ATKINSON, G. F., 1911, The origin and taxonomic value of the veil in Dictyophora and Ithyphallus, *Botan. Gaz.*, **51**: 1–20, *f. 1*, *pl. 1–7*.

———, 1914, The development of Lepiota clypeolaria, *Ann. Myc.*, **12**: 346–356, *pl. 13–16*.

———, 1914*a*, The development of Agaricus arvensis and A. comtulus, *Amer. Jour. Botany*, **1**: 3–22, *pl. 1–2*.

———, 1914*b*, The development of Amanitopsis vaginata, *Ann. Myc.*, **12**: 369–392, *pl. 17–19*.

———, 1914*c*, The development of Armillaria mellea, *Myc. Centralbl.*, **4**: 113–121, *pl. 1, 2*.

———, 1915, Homology of the universal veil in Agaricus, *Myc. Centralbl.*, **5**: 13–19, *pl. 3*.

———, 1915*b*, Morphology and development of Agaricus Rodmani, *Proc. Amer. Phil. Soc.*, **54**: 309–343, *pl. 7–13*.

———, 1915*c*, Phylogeny and relationships in the Ascomycetes, *Ann. Missouri Bot. Gard*, **2**: 315–376.

———, 1916, Origin and development of the lamellae in Coprinus, *Botan. Gaz.*, **61**: 89–130, *pl. 5–12*.

———, 1918, The genus Endogone, *Mem. Brooklyn Bot. Gard.*, **1**: 1–17.

BACCARINI, P., 1906, Appunti per la morfologia dello stroma nei Dotidacei, *Ann. Botanica*, **4**: 195–211, *pl. 7*.

BACHMAN, F. M., 1912, A new type of spermogonium and fertilization in Collema, *Ann. Botany*, **26**: 747–760. *1 pl.*

———, 1913, The origin and development of the apothecium in Collema pulposum, *Arch. Zellforsch.*, **10**: 369–430, *pl. 30–36*.

BACHMANN, E., 1923, Über das Verhältnis der Konidien zum Flechtenpilz, *Hedwigia*, **64**: 233–255.

BACHMANN, H., 1900, Mortierella van-Tieghemi n. sp., *Jahrb. Wiss. Botanik*, **34**: 279–328, *pl. 9–10*.

BAGCHEE, K., 1925, Cytology of the Ascomycetes, Pustularia bolarioides, *Ann. Botany*, **39**: 217–266, *pl. 5–8*.

BAINIER, G., 1909, Monographie des Chaetomium et des Chaetomidium, *Bull. Soc. Myc. France*, **25**: 191–237, *pl. 10–26*.

BAIRD, E. A., 1924, The structure and behavior of the nucleus in the life history of Phycomyces nitens (Agardh) Kuntze and Rhizopus nigricans Ehrbg., *Trans. Wisconsin Acad. Sci.* **21**: 357–380, *pl. 14–15*.

BALLY, W., 1912, Cytologische Studien an Chytridineen, *Jahrb. Wiss. Botanik*, **50**: 95–156, *pl. 1–5*.

BAMBEKE, C. VAN, 1902, Le mycélium de Lepiota meleagris, *Mém. Acad. R. Sci. Belgique*, **54**: 1–57, *pl. 1–7*.

———, 1904, Sur l'évolution nucléaire et la sporulation chez Hydnangium carneum Wallr., *Mém. Acad. R. Sci., Belgique*, **54**: 1–44, *pl. 1–3*.

———, 1910, La relation du mycélium avec le carpophore chez Ithyphallus impudicus (L.) Sacc. et Mutinus caninus (Huds.) Fries, *Mém. Acad. R. Belgique, Cl. d. Sci. sér.* 2., 2^8: 1–26, *pl. 1–4*.

———, 1915, Recherches sur certains éléments du mycélium d' Ithyphallus, *Bull. Cl. d. Sci. Acad. R. Belgique*, **1914**: 167–175. *1 pl.*

BARKER, B. T. P., 1900, A fragrant "Mycoderma" yeast, *Ann. Botany*, **14**: 215–244, *pl. 13*.

———, 1901, A conjugating yeast, *Phil. Trans. R. Soc. London, B*, **194**: 467–485.

———, 1903, The morphology and development of the ascocarp in Monascus, *Ann. Botany*, **17**: 167–236, *pl. 12–13*.

———, 1904, Further observations on the ascocarp of Rhyparobius, *British Ass. Adv. Sci. Rept.* **1904**: 825–826.

BARRETT, J. T., 1912, Development and sexuality in some species of Olpidiopsis, *Ann. Botany*, **26**: 209–238, *pl. 23–26*.

———, 1912*a*, The development of Blastocladia strangulata n. sp., *Botan. Gaz.*, **54**: 353–371, *pl. 18–20*.

BARTLETT, A. W., 1926, On a new species of Urophlyctis producing galls on Lotus corniculatus Linn., *Trans. British Myc. Soc.*, **11**: 266–281, *pl. 11–14*.

BARY, A. DE, 1863, Recherches sur le développement de quelques champignons parasites, *Ann. Sci. Nat. Botanique*, 4 sér., **20**: 5–148, *pl. 1–13*.

———, 1881, Zur Kenntnis der Peronosporeen, *Botan. Zeitung*, **39**: 521–530, 537–544, 553–563, 569–578, 585–595, 601–609, 617–626, *pl. 5*.

———, 1881, Untersuchungen über die Peronosporeen und Saprolegnieen und die Grundlagen eines natürlichen Systems der Pilze, *Abhandl. Senckenb. Naturf. Ges.*, **12**: 225–370.

———, 1884, Vergleichende Morphologie und Biologie der Pilze, Mycetozoen, und Bacterien, Leipzig, 558 p.

BATAILLE, F., 1910, Flore monographique des Hygrophores, *Mém. Soc. d'Émul Doubs 8 sér.*, **4**: 131–191 [1909] .

BAUCH, R., 1922, Kopulationsbedingungen und sekundäre Geschlechtsmerkmale bei Ustilago violacea, *Biol. Centralbl.*, **42**: 9–38.

———, 1923, Uber Ustilago longissima und ihre Varietät macrospora, *Zeitschr. f. Botanik*, **15**: 241–279, *pl. 3*.

———, 1925, Untersuchungen über die Entwicklungsgeschichte und Sexual-physiologie der Ustilago bromivora und Ustilago grandis, *Zeitschr. f. Botanik*, **17**: 129–177, *4 fig.*

———, 1926, Untersuchungen über zweisporige Hymenomyzeten I. Haploide Parthenogenesis bei Camarophyllus virgineus, *Zeitschr. f. Botanik*, **18**: 337–387, *pl. 2–3*.

———, 1927, Untersuchungen über zweisporige Hymenomyceten II. Kerndegeneration bei einigen Clavaria-Arten, *Arch. f. Protistenk.*, **58**: 285–299, *pl. 3–4*.

BAUR, E., 1898, Zur Frage nach der Sexualität der Collemaceen, *Ber. Deutsch. Botan. Ges.*, **16**: 363–367, *pl. 23*.

———, 1901, Die Anlage und Entwicklung einiger Flechtenapothecien, *Flora*, **88**: 319–332.

———, 1904, Untersuchungen über die Entwicklungsgeschichte der Flechtenapothecien I, *Botan. Zeitung.*, **62**: 21–44, *pl. 1–2*.

BEELI, M., 1920, Note sur le genre Meliola, *Bull. Jard. Botan. Bruxelles*, **7**: 89–160.

BEER, R., 1911, Notes on the development of the carpophore of some Agaricaceae, *Ann. Botany*, **25**: 683–689, *pl. 52*.

BELL, H. P., 1924, Fern rusts of Abies, *Botan. Gaz.*, **77**: 1–30, *pl. 1–5*.

BENSAUDE, M., 1918, Recherches sur le cycle évolutif et la sexualité chez les Basidiomycètes, *Thèse* [Paris], 153 p.

BERKELEY, M. J., 1843, On two hymnomycetous fungi belonging to the Lycoperdaceous group, *Hooker's Jour. Botany*, **2**: 200.

BERLESE, A. N., 1891, Interno allo sviluppo di due nuove Ipocreacei, *Malpighia*, **5**: 386–418, *pl. 29–30*.

———, 1898, Über die Befruchtung und Entwicklung der Oosphäre bei den Peronosporeen, *Jahrb. Wiss. Botanik*, **31**: 159–196, *pl. 4–7*.

BERNARD, C., 1908, Quelques mots sur Aseroë rubra la Bill. var. Junghuhnii Schlecht., *Ann. Jard. Bot. Buitenzorg*, **22**: 224–238, *pl. 25–26*.

BESSEY, C. E., 1887, The growth of Tulostoma mammosum, *Amer. Nat.* **21**: 665–666.

———, 1903, The structure and classification of the Phycomycetes, *Trans. Amer. Microsc. Soc.*, **24**: 27–54.

BESSEY, E. A., 1914, Some suggestions as to the phylogeny of the Ascomycetes, *Myc. Centralbl.*, **3**: 149–153.

BETTS, A. D., 1912, A beehive fungus, Pericystis alvei gen. et spec. nov., *Ann. Botany*, **26**: 795–799, *pl. 75, 76.*

BETTS, E. M., 1926, Heterothallism in Ascobolus carbonarius, *Amer. Jour. Botany* [1927], **13**: 427–432.

BEZSONOV, N., 1913, Notice sur le développement des conidiophores et sur le phénomenes nucléaires qui l'accompagnent chez le Sphaerotheca Mors-uvae (Schwein.) Berk. & Curt. et le Microsphaera Astragali, [s. Erysiphe Astr.] (DC.) Trev., *Bull. Soc. Myc. France*, **29**: 279–291, *pl. 14–19.*

———, 1914, Quelques nouveaux faits concernant la formation du perithèce et la délimitation des ascospores chez les Erysiphacées, *Bull. Soc. Myc. France*, **30**: 406–415, *pl. 27–30.*

———, 1919, Über die Züchtung von Pilzen auf hochkonzentrierten rohrzuckerhaltigen Nährböden und über die Chondriomfrage, *Ber. Deutsch. Botan. Ges.*, **37**: 136–148, *pl. 2.*

BIFFEN, R. H., 1899, On the biology of Agaricus velutipes Curt. (Collybia velutipes P. Karst.), *Jour. Linn. Soc. Botany*, **34**: 147–162, *pl. 2–4.*

———, 1901, On the biology of Bulgaria polymorpha Wett., *Ann. Botany*, **15**: 119–134, *pl. 7.*

BIOURGE, P., 1923, Les moisissures du groupe Penicillium, *La Cellule*, **33**: 1–331, *pl. 1–22, col. pl. 1–13.*

BLACKMAN, V. H., 1904, On the fertilization, alternation of generations and general cytology of the Uredineae, *Ann. Botany*, **18**: 323–373, *pl. 21–24.*

BLACKMAN, V. H., and H. C. I. FRASER, 1905, Fertilization in Sphaerotheca, *Ann. Botany*, **19**: 567–569.

———, 1906, On the sexuality and development of the ascocarp of Humaria granulata, *Proc. R. Soc. London, B*, **77**: 354–368.

———, 1906*a*, Further studies on the sexuality of the Uredineae, *Ann. Botany*, **20**: 35–48, *pl. 3–4.*

BLACKMAN, V. H., and E. J. WELSFORD, 1912, The development of the perithecium of Polystigma rubrum DC., *Ann. Botany*, **26**: 761–767, *pl. 70–71.*

BLAKESLEE, A. F., 1904, Sexual reproduction in the Mucorineae, *Proc. Amer. Acad. Arts. Sci.*, **40**: 205–319, *pl. 1–4.*

———, 1906, Zygospore germinations in the Mucorineae, *Ann. Myc.*, **4**: 1–28.

———, 1913, Conjugation in the heterogamic genus Zygorhynchus, *Myc. Centralbl.*, **2**: 241–244, *pl. 1–2.*

———, 1915, Sexual reactions between hermaphroditic and dioecious Mucors, *Biol. Bull.*, **29**: 87–98, *pl. 1–3.*

BLAKESLEE, A. F., and others, 1921, Sexual dimorphism in Cunninghamella, *Botan. Gaz.*, **72**: 185–219.

———, 1927, Sexual dimorphism in Mucorales, *Botan. Gaz.*, **84**: 27–57.

BLIZZARD, A. W., 1917, The development of some species of agarics, *Amer. Jour. Botany*, **4**: 221–240, *pl. 6–11.*

BLOMFIELD, J. E., and E. T. SCHWARTZ, 1910, Some observations in the tumors of Veronica Chamaedrys caused by Sorosphaera Veronicae, *Ann. Botany*, **24**: 35–43, *pl. 5.*

BLUMER, S., 1922, Beiträge zur Spezialisation der Erysiphe horridula Lév. auf Borraginaceen, *Centralbl. Bakt. II Abt.*, **55**: 480–506.

———, 1922, Die Formen der Erysiphe cichoracearum DC., *Centralbl. Bact. II Abt.*, **57**: 45–60.

BOAS, F., 1915, Über ein neues koremienbildendes Penicillium, *Myc. Centralbl.*, **5**: 73–83.

———, 1916, Mykologische Notizen, *Centralbl. Bakt. II Att.*, **44**: 695–701.

BONNS, W. W., 1922, A preliminary study of Claviceps purpurea in culture, *Amer. Jour. Botany*, **9**: 339–353. *pl. 16–21.*

BOUDIER, E., 1907, Histoire et classification des Discomycètes d'Europe [Paris], 221 p.

BOULANGER, E., 1893, Matruchotia varians, *Rev. Gén. Botanique*, **5**: 401–406, *pl. 12–14.*

———, 1897, Sur une forme conidienne nouvelle dans le genre Chaetomium, *Rev. Gén. Botanique*, **9**: 17–26, *pl. 1–3.*

BREFELD, O., 1872, Mucor Mucedo, Chaetocladium Jonesii, Piptocephalis Freseniana, Zygomyceten, *Botan. Unters. ü. Schimmelpilze*, **1**: 1–64, *pl. 1–6.*

———, 1874, Die Entwicklungsgeschichte von Penicillium, *Botan. Unters. ü. Schimmelpilze*, **2**: 1–98, *pl. 1–8.*

———, 1877, Basidiomyceten I, *Bot. Unters. ü. Schimmelpilze*, **3**: 1–226, *pl. 1–11.*

———, 1881, *Botan. Unters. ü. Schimmelpilze*, **4**: 1–191, *pl.* 1–10.

———, 1883, Die Brandpilze I, *Botan. Unters ü. Schimmelpilze*, **5**: 1–220, *pl. 1–13.*

———, 1884, Botanische Untersuchungen über Myxomyceten und Entomophthoreen, *Unters. Ges. Geb. Myk.*, **6**: 1–78, *pl. 1–5.*

———, 1888, Basidiomyceten II, Protobasidiomyceten, *Unters. Ges. Geb. Myk.*, **7**: 1–178, *pl. 1–11.*

———, 1889, Basidiomyceten III, Autobasidiomyceten und die Begründung des natürlichen Systemes der Pilze, *Unters. Ges. Geb. Myk.*, **8**: 1–305, *pl. 1–12.*

———, 1891, Die Hemiasci und die Ascomyceten, *Unters. Ges. Geb. Myk.*, **9**: 1–156, *pl. 1–4.*

———, 1891, Ascomyceten II, *Unters. Ges. Geb. Mykol.*, **10**: 157–378, *pl. 1–10.*

———, 1895, Die Brandpilze II, Die Brandkrankheiten des Getreides, *Unters. Ges. Geb. Myk.*, **11**: 1–98, *pl. 1–5.*

———, 1895, Die Brandpilze III, Hemibasidii, *Unters. Ges. Geb. Myk.*, **12**: 99–236, *pl. 6–12.*

———, 1908, Die Kultur der Pilze und die Anwendung der Kulturmethoden für die verschiedenen Formen der Pilze nebst Beiträgen zur vergleichenden Morphologie der Pilze und der natürlichen Wertschätzung ihrer zugehörigen Fruchtformen, *Unters. Ges. Geb. Myk.*, **14**: 1–256.

———, 1912, Die Brandpilze und die Brandkrankheiten V, mit ausschliessenden Untersuchungen der niederen und der höheren Pilze, *Unters. Ges. Geb. Myk*, **15**: 1–151, *pl. 1–7.*

BREFELD, O. and R. FALCK, 1905, Die Brandpilze IV, Die Bluteninfektion bei den Brandpilzen und die natürlichen Verbreitung der Brandkrankheiten, *Unters. Ges. Geb. Myk.*, **13**: 1–75, *pl. 1–2.*

BRIERLEY, W. B., 1913, The structure and life history of Leptosphaeria Lemaneae, *Mem. Proc. Manchester Lit. Phil. Soc.*, **57**[8]: 1–24, *2 pl.*

———, 1915, The endoconidia of Thielavia basicola, *Ann. Botany*, **29**: 483–493, *pl. 23.*

———, 1917, Spore germination in Onygena equina, *Ann. Botany*, **31**: 127–132.

BRONSART, H. VON, 1919, Vergleichende Untersuchungen über drei Xylariaarten, *Centralbl. Bact. II Abt.*, **49**: 51–76, *1 pl.*

BROOKS, F. T., 1910, The development of Gnomonia erythrostoma Pers., *Ann. Botany*, **24**: 585–605, *pl. 48–49.*

———, 1911, Silver leaf disease, *Jour. Agr. Sci.*, **4**: 133–144, [1913] **5**: 288–308, *pl. 12.*

BROWN, H. B., 1913, Studies in the development of Xylaria, *Ann. Myc.*, **11**: 1–13, *pl. 1–2.*

BROWN, W. H., 1910, The development of the ascocarp of Leotia, *Botan. Gaz.*, **50**: 443–459.

———, 1911, The development of the ascocarp of Lachnea scutellata, *Botan. Gaz.*, **52**: 275–305, *pl. 9.*

———, 1915, The development of Pyronema confluens var. inigneum, *Amer. Jour. Botany*, **2**: 289–298.

BRUNSWIK, H., 1924, Über die Sexualitätsverhältnisse bei den Basidiomyceten, *Verh. zool.-bot. Ges. Wien.* [1923], **73**: 153–154.

———1924*a*, Neuere Untersuchungen über die Sexualitätsverhältnisse bei den Pilzen, *Zeitschr. Ind. Abstamm.-und Vererb.*, **34**: 214–228.

———, 1924*b*, Untersuchungen über die Geschlechts- und Kernverhältnisse bei der Hymenomyzeten-gattung Coprinus, *Botan. Abhandl.*, [Goebel], **5**: 1–152.

———, 1926, Die Reduktionsteilung bein den Basidiomyzeten, *Zeitschr. f. Botanik*, **18**: 481–498.

BUCHANAN, R. E., 1910, Monascus purpureus in silage, *Mycologia*, **2**: 99–106, *pl. 22, 23.*

BUCHOLTZ, F., 1897, Bemerkung zur systematischen Stellung der Gattung Meliola, *Bull. Herb. Boissier* 2 *sér.*, **5**: 627–630, *pl. 22.*

———, 1897, Zur Entwicklungsgeschichte der Tuberaceen, *Ber. Deutsch. Botan. Ges.*, **15**: 211–226, *pl. 6.*

———, 1901, Hypogaeen aus Russland, *Hedwigia*, **40**: 304–322.

———, 1902, Beiträge zur Morphologie und Systematik der Hypogäen nebst Beschreibung aller bis jetzt in Russland angetroffenen Arten, *Izdan. Estestvenno-Istor. Muz. graf. E. P. Sheremetev, Mikhailovsk, Moskva*, **1**: 1–196. *pl. 1–5.*

———, 1903, Zur Morphologie und Systematik der Fungi hypogaei, *Ann. Myc.*, **1**: 152–174, *pl. 4–5.*

———, 1908, Zur Entwicklung der Choiromyces-Fruchtkörper, *Ann. Myc.*, **6**: 539–550, *pl. 23.*

———, 1910, Zur Entwicklungsgeschichte des Balsamieenfruchtkörpers, nebst Bemerkungen zue Vernandschaft der Tuberineen, *Ann. Myc.*, **8**: 121–141, *pl. 1.*

———, 1911, Über die Befruchtung von Endogone lactiflua Berk., *Ann. Myc.*, **9**: 329–330.

———, 1912, Beiträge zur Kenntnis der Gattung Endogone, *Beih. Botan. Centrabl.* II *Abt.*, **29**: 147–225. [Resumé of Neue Beiträge zur Morphologie und Cytologie der untererdischen Pilze, Fungi hypogaei I, Die gattung Endogone, *Izdan. Estestvenno-Istor. Muz. graf. E. P. Sheremetev, Mickhailovsk, Moskva*, **9**: 1–108, *pl. 1–8.* 1911.]

BUDDIN, W. and E. M. WAKEFIELD, 1927, Studies on Rhizoctonia Crocorum (Pers.) DC. and Helicobasidium purpureum (Tul.) Pat., *Trans. British Myc. Soc.*, **12**: 116–140, *pl. 11–14.*

BUDER, J., 1916, Zur Frage des Generationswechsels im Pflanzenreiche, *Ber. Deutsch. Botan. Ges.*, **34**: 559–576.

BÜREN, G. VON, 1915, Die schweizerischen Protomycetaceen mit besonderer Berücksichtigung ihrer Entwicklungsgeschichte und Biologie, *Beitr. Krypt. fl. d. Schweiz.*, **5**: 1–95, *pl. 1–7.*

———, 1917, Beitrag zur Kenntnis des Myzels der Gattung Volkartia, R. Maire (v. Buren), *Mitt. Naturf. Ges. Bern.*, **1916**: 112–123, *pl. 1.*

———, 1918, Beitrag zur Biologie und Entwicklungsgeschichte von Protomyces inundatus Dang., *Mitt. Naturf. Ges. Bern.*, **1917**: 109–132, *1 pl.*

———, 1922, Weitere Untersuchungen über die Entwicklungsgeschichte und Biologie der Protomycetaceen, *Beitr. Krypt. fl. d. Schweiz*, **5**[3]: 1–94.

BULLER, A. H. R., 1909–1924, Researches on fungi **1**: 1–287, 1909; **2**: 1–492, 1922; **3**: 1–611, 1924.

———, 1910, The Functions and the fate of the cystidia of Coprinus atramentarius, together with some general remarks on Coprinus fruit-bodies, *Ann. Botany*, **24**: 613–629, *pl. 50, 51.*

———, 1915, Die Erzeugung und Befreiung der Sporen bei Coprinus sterquilinus, *Jahrb. Wiss. Botanik*, **56**: 299–399.

BURGEFF, H., 1912, Über Sexualität, Variabilität und Vererbung bei Phycomyces nitens, *Ber. Deutsch. Botan. Ges.*, **30**: 679–685.

BURGEFF, H., 1915, Untersuchungen über Variabilität, Sexualität und Erblichkeit bei Phycomyces nitens Kuntze II, *Flora*, **108**: 353–448.

———, 1920, Über den Parasitismus von Chaetocladium, *Zeitschr. f. Botanik*, **12**: 1–35.

———, 1920*a*, Sexualität und Parasitismus bei Mucorineen, *Ber. Deutsch. Botan. Ges.*, **38**: 318–327.

———, 1924, Untersuchungen über Sexualität und Parasitismus bei Mucorineen I, *Botan. Abh.* [Goebel], **4**: 1–135.

BURKHOLDER, W. H., 1917, The perfect stage of Gloeosporium venetum, *Phytopathology*, **7**: 83–91.

BURT, E. A., 1894, A North American Anthurus, its structure and development, *Mem. Boston Soc. Nat. Hist.*, **3**: 487–505, *pl. 49–50.*

———, 1896, The development of Mutinus caninus, *Ann. Botany*, **10**: 343–372, *pl. 17–18.*

———, 1896, The Phalloideae of the United States I, Development of the receptaculum of Clathrus columnatus Bosc, *Botan. Gaz.*, **22**: 273–292, *pl. 11, 12.*

———, 1897, The Phalloideae of the U. S. III, *Botan. Gaz.*, **24**: 73–92.

———, 1914, The Thelephoraceae of North America I, Thelphora, *Ann. Mo. Botan. Gard.*, **1**: 185–228, *pl. 4–5.*

———, 1914*a*, The Thelephoraceae of North America II, Craterellus, *Ann. Mo. Botan. Gard.*, **1**: 327–350, *pl. 15–17.*

———, 1914*b*, The Thelephoraceae of North America III, Craterellus borealis and Cyphella., *Ann. Mo. Botan. Gard.*, **1**: 357–382, *pl. 19.*

———, 1915, The Thelephoraceae of North America IV, Exobasidium, *Ann. Mo. Botan. Gard.*, **2**: 627–658, *pl. 21.*

———, 1915*a*, The Thelephoraceae of North America V, Tremellodendron, Eichleriella and Sebacina, *Ann. Mo. Botan. Gard*, **2**: 731–770, *pl. 26–27.*

———, 1916, The Thelephoraceae of North America VI, Hypochnus, *Ann. Mo. Botan. Gard.*, **3**: 203–241.

———, 1916*a*, The Thelephoraceae of North America VII, Septobasidium, *Ann. Mo. Botan. Gard.*, **3**: 319–343.

———, 1917, The Thelephoraceae of North America VIII, Coniophora, *Ann. Mo. Botan. Gard.*, **4**: 237–269.

———, 1917*a*, Merulius in North America, *Ann. Mo. Bot. Gard.*, **4**: 305–362, *pl. 20–22*, Supplementary . . . notes *Ibid* [1919], **6**: 143–145.

———, 1918, The Thelephoraceae of North America IX, Aleurodiscus, *Ann. Mo. Botan. Gard.*, **5**: 177–203.

———, 1918*a*, The Thelephoraceae of North America X, Hymenochaete, *Ann. Mo. Botan. Gard.*, **5**: 301–372.

———, 1919, The Thelephoraceae of North America XI. Tulasnella, Veluticeps, Mycobonia, Epithele, and Lachnocladium, *Ann. Mo. Botan. Gard.*, **6**: 253–280.

———, 1919*a*, Protomerulius Farlowii Burt, n. sp., *Ann. Mo. Botan. Gard.* **6**: 175–177.

———, 1920, The Thelephoraceae of North America XII, Stereum, *Ann. Mo. Botan. Gard*, **7**: 81–248.

———, 1924, The Thelephoraceae of North America XIII, Cladoderris, Hypolyssus, Cymatella, Skepperia Cytidia, Solenia, Matruchotia, Microstroma, Protocoronospora, and Asterostroma, *Ann. Mo. Botan. Gard.* **11**: 1–36.

———, 1925, The Thelephoraceae of North America XIV, Peniophora, *Ann. Mo. Botan. Gard.*, **12**: 213–357.

———, 1926, The Thelephoraceae of North America XV, Corticium, *Ann. Mo. Botan. Gard.*, **13**: 173–354.

BÜSGEN, M., 1882, Die Entwicklung der Phycomycetensporangien, *Jahrb. Wiss. Botanik*, **13**: 253–285, *pl. 12.*

———, 1887, Beitrag zur Kenntnis der Cladochytrien, *Beitr. Biol. Pfl.*, [Cohn], **4**: 269–283, *pl. 15.*

BUTLER, E. J., 1907, An account of the genus Pythium and some Chytridiaceae, *Mem. Dept. Agr. India*, **1**[5]: 1–160.

———, 1910, The wilt disease of pigeon-pea and pepper, *Mem. Dept. Agr. India, Bot. ser.*, **2**: 1–64.

———, 1911, On Allomyces, a new aquatic fungus, *Ann. Botany*, **25**: 1023–1034, *f. 1–18.*

———, 1913, Studies in the Peronosporaceae II, Pythium debaryanum Hesse, *Mem. Dept. Agr. India*, **5**: 262–267, *pl. 5.*

BUTLER, E. J., and C. S. KULKARNI, 1913, Studies in the Peronosporaceae, Colocasia blight caused by Phytophthora Colocasiae Rac., *Mem. Dept. Agr. India*, **5**: 233–261, *pl. 1–4.*

CARRUTHERS, D., 1911, Contributions to the cytology of Helvella crispa, *Ann. Botany*, **25**: 243–252, *pl. 18–19.*

CAVARA, F., 1899, Osservazioni citologiche sulle Entomophthoreae, *N. Giorn. Botan. Ital. N. S.* **6**: 411–466, *pl. 4–5.*

———, 1905, Causeries mycologiques, *Ann. Myc.*, **3**: 362–365.

CAVARA, F., and N. MOLLICA, 1907, Ricerche intorno al ciclo evolutivo di una interessante forma di Pleospora herbarum (Pers.) Rabenh., *Ann. Myc.*, **5**: 119–149.

CAVERS, F., 1915, The interrelationship of protista and primitive fungi, *New Phytologist*, **14**: 94–104; 164–168; 223–227; 275–280; 302–304.

CAYLEY, D. M., 1921, Some observations on the life history of Nectria galligena, *Ann. Botany*, **35**: 79–92, *pl. 4–5.*

———, 1923, The phenomenon of mutal aversion between mono-spore mycelia of the same fungus (Diaporthe perniciosa Marshall) with a discussion of sex heterothallism in fungi, *Jour. Genetics*, **13**: 353–370.

CHIVERS, A. H., 1915, A monograph of the genera Chaetomium and Ascotricha, *Mem. Torrey Botan. Club*, **14**: 155–240, *pl. 6–16.*

CHRISTMAN, A. H., 1905, Sexual reproduction in the rusts, *Botan. Gaz.*, **39**: 267–275, *p*[1]. *8.*

———, 1907, The alternation of generations and the morphology of the spore forms in the rusts, *Botan. Gaz.*, **44**: 81–101, *pl. 7.*

———, 1907*a*, The nature and development of the primary uredospore, *Trans. Wisconsin Acad. Sci.*, **15**: 517–524, *pl. 29.*

CLAUSSEN, P., 1905, Zur Entwicklungsgeschichte der Ascomyceten, Boudiera, *Botan. Zeitung*, **63**: 1–27, *pl. 1–3.*

———, 1906, Über neuere Arbeiten zur Entwicklungsgeschichte der Ascomyceten, *Ber. Deutsch. Botan. Ges.*, **24**: 11–38.

———, 1907, Zur Kenntnis der Kernverhältnisse von Pyronema confluens, *Ber. Deutsch. Botan. Ges.*, **25**: 586–590.

———, 1908, Über Eientwicklung und Befruchtung bei Saprolegnia monoica, *Ber. Deutsch. Botan. Ges.*, **26**: 144–161.

———, 1912, Zur Entwicklungsgeschichte der Ascomyceten, Pyronema confluens, *Zeitschr. f. Botanik*, **4**: 1–63, *pl. 1–6.*

———, 1921, Entwicklungsgeschichtliche Untersuchungen über den Erreger der als Kalkbrut bezeichneten Krankheit der Bienen, *Arb. Biol. Reichsanst. Land.-Forstw.*, **10**: 467–521.

CLINTON, G. P., 1902, Cladochytrium Alismatis, *Botan. Gaz.*, **33**: 49–61, *pl. 2–4.*

COKER, W. C., 1914, Two new species of water molds, *Mycologia*, **6**: 285–301, *pl. 146–148.*

COKER, W. C., 1920, Notes on the lower Basidiomycetes of North Carolina, *Jour. Elisha Mitchell Sci. Soc.*, **35**: 113–182.

———, 1923, The Saprolegniaceae with notes on other water molds, Chapel Hill, N. C., 201 p., *63 pl.*

COKER, W. C., and J. N. COUCH, 1924, Revision of the genus Thraustotheca with a description of a new species, *Jour. Elisha Mitchell Sci. Soc.*, **40**: 197–202, *pl. 38–40.*

COKER, W. C., and F. A. GRANT, 1922, A new genus of water mold related to Blastocladia, *Jour. Elisha Mitchell Sci. Soc.*, **37**: 180–182.

COKER, W. C., and O. W. HUMAN, 1912, Thraustotheca clavata, *Mycologia*, **4**: 87–90, *pl. 63.*

COKER, W. C., and L. WILSON, 1911, Schizosaccharomyces octosporus, *Mycologia*, **3**: 283–287, *pl. 55.*

COLLEY, R. H., 1918, Parasitism, morphology and cytology of Cronartium ribicola, *Jour. Agr. Res.*, **15**: 619–660, *pl. 48–59.*

CONARD, H. S., 1913, The structure of Simblum, *Mycologia*, **5**: 264–273, *pl. 96, 97.*

———, 1915, The structure and development of Secotium agaricoides, *Mycologia*, **7**: 94–104, *pl. 157.*

COOK, M. T., 1923, The life-history of Nectria Ipomoeae, *Mycologia*, **15**: 233–235, *pl. 25.*

COOK, W. R. I., 1926, The genus Ligniera Maire and Tison, *Trans. British Myc. Soc.*, **11**: 196–213, *pl. 8–9.*

COOL, C., 1912, Beiträge zur Kenntnis der Sporenkeimung und Reinkulture der höheren Pilze, *Mededeel. Phytopath. Lab. W. C. Scholten*, **3**: 5–38.

COTTON, A. D., 1914, The genus Atichia, *Kew Bull. Misc. Inf.*, **1914**: 54–63.

COUCH, J. N., 1924, Some observations on spore formation and discharge, in Leptolegnia, Achlya, and Aphanomyces, *Jour. Elisha Mitchell Sci. Soc.*, **40**: 27–42.

———, 1926, Heterothallism in Dictyuchus, a genus of water moulds, *Ann. Botany*, **40**: 849–881, *pl. 35–38.*

———, 1927, Some new water fungi from the soil with observations on spore formation, *Jour. Elisha Mitchell Sci. Soc.*, **35**: 227–242, *pl. 37–43.*

CRAIGIE, J. H., 1927, Experiments on sex in rust fungi, *Nature*, **120**: 116–117, *1 fig.*

CUNNINGHAM, G. H., 1924, The development of Gallacea Scleroderma (Cke.) Lloyd, *Trans. British Myc. Soc.*, **9**: 193–200, *pl. 9–10.*

———, 1925, The development of two species of Secotium, *Trans. British Myc. Soc.*, **10**: 216–224, *pl. 11–12.*

———, 1927, The development of Geaster velutinus, *Trans. British Myc. Soc.*, **12**: 12–20, *9 fig.*

———, 1927*a*, Development of Lycoperdon depressum, *New Zealand Jour. Sci. Technol.*, **8**: 228–232. *8 fig.*

CURTIS, K. M., 1921, The life history and cytology of Synchytrium endobioticum [Schilb.] Perc., the cause of wart disease in potato, *Phil. Trans. R. Soc. London, B.*, **210**: 409–478, *pl. 12–16.*

CUTTING, E. M., 1909, On the sexuality and development of the ascocarp in Ascophanus carneus Pers., *Ann. Botany*, **23**: 399–417, *pl. 28.*

DALE, E., 1903, Observations on Gymnoascaceae, *Ann. Botany*, **17**: 571–596, *pl. 27, 28.*

———, 1909, On the morphology and cytology of Aspergillus repens, *Ann. Myc.*, **7**: 215–225, *pl. 2, 3.*

DANGEARD, P. A., 1889, Mémoire sur les Chytridinées, *Le Botaniste*, **1**: 39–74, *pl. 2, 3.*

———, 1891, Recherches histologiques sur les champignons, *Le Botaniste*, **2**: 63–149, *pl. 3–7.*

———, 1892, Recherches sur la réproduction sexuelle des champignons, *Le Botaniste*, **3**: 221–286, *pl. 20–23.*

DANGEARD, P. A., 1894, La réproduction sexuelle des Ascomycètes, *Le Botaniste*, **4**: 21–61.
———, 1894*a*, La truffe, *Le Botaniste*, **4**: 63–87.
———, 1895, Mémoire sur la réproduction sexuelle des Basidiomycètes, *Le Botaniste*, **4**: 119–181.
———, 1895*a*, Mémoire sur les parasites du noyau et du protoplasma, *Le Botaniste*, **4**: 199–248.
———, 1897, Second mémoire sur la réproduction sexuelle des Ascomycètes, *Le Botaniste*, **5**: 245–284.
———, 1900, Recherches sur la structure du Polyphagus Euglenae, *Le Botaniste*, **7**: 213–258, *pl. 6, 7*.
———, 1903, Un nouveau genre des Chytridiacées, *Ann. Myc.*, **1**: 61–64, *pl. 2*.
———, 1906, Nouvelles considérations sur la réproduction sexuelle des champignons supérieurs, *Le Botaniste*, **9**: 35–46.
———, 1906, Recherches sur le développement du périthèce chez les Ascomycètes, *Le Botaniste*, **9**: 59–303, *pl. 1–18*.
———, 1907, L'origine du périthèce chez les Ascomycètes, *Le Botaniste*, **10**: 1–385, *pl. 1–91*.
DARBISHIRE, O. V., 1900, Über die Apothecienentwicklung der Flechte Physcia pulverulenta, *Jahrb. Wiss. Botanik.*, **34**: 329–345.
DASTUR, J. F., 1913, On Phytophthora parasitica n. sp., *Mem. Dept. Agr. India*, **5**: 177–231.
———, 1921, Cytology of Tilletia Tritici (Bjerk.) Winter, *Ann. Botany*, **35**: 399–407, *pl. 20*.
DAVIS, B. M., 1900, The fertilization of Albugo candida, *Botan. Gaz.*, **29**: 297–311, *pl. 22*.
———, 1903, Oogenesis in Saprolegnia, *Botan. Gaz.*, **35**: 233–249; 320–349, *pl. 9, 10*.
———, 1904, The relationships of sexual organs in plants, *Botan. Gaz.*, **38**: 241–264.
DAVIS, J., 1925, Studies on Ophiobolus graminis Sacc., the take-all disease of wheat, *Jour. Agr. Res.*, **31**: 801–825, *pl. 1–6*.
DAWSON, M., 1900, On the biology of Poronia punctata, *Ann. Botany*, **14**: 245–262, *pl. 14, 15*.
DELITSCH, H., 1926, Zur Engwicklungsgeschichte der coprophilen Ascomyceten: Lasiobolus pulcherrimus Crouan; Humaria anceps Rehm, var. aurantiaca, n. var.; und Sporormia leporina Niessl, *Diss.* Leipzig, 40 p.
DEMELIUS, P., 1911, Beitrag zur Kenntnis der Cystiden, *Verh. Zool.-Botan. Ges. Wien*, **61**: 278–287; **62**: 97–124; **65**: 36–47, *pl. 1, 2*.
DIEDICKE, H., 1915, Pilze VII, *Krypt. fl. d. Mark Brandenburg* [Leipzig], **9**: 962 p.
DIETEL, P., 1903, Über die auf Leguminosen lebenden Rostpilze und die Verwandschaftsverhältnisse der Gattungen Pucciniaceen, *Ann. Myc.*, **1**: 3–14.
———, 1904, Betrachtungen über die Verteilung der Uredineen auf ihren Nährpflanzen, *Centralbl. Bact. II Abt.*, **12**: 218–234.
———, 1906, Monographie der Gattung Ravenelia, *Beih. Bot. Centrabl. II Abt.*, **20**: 343–413, *pl. 5, 6*.
———, 1908, Über die morphologische Bewertung der gleichnamigen Sporenformen in verschiedenen Gattungen der Uredineen, *Hedwigia*, **48**: 118–125.
———, 1912*a*, Über die Abschleuderung der Sporidien bei den Uredineen, *Myc. Centralbl.*, **1**: 355–359.
———, 1912, Über die Verwandtschaftsbeziehungen der Rostpilzgattungen Kuehneola und Phragmidium, *Ann. Myc.*, **10**: 205–213.
———, 1915, Betrachtungen zur Systematik der Uredineen I, *Myc. Centralbl.* **5**: 65–73.
———, 1918, Über die wirtswechselnden Rostpilze, *Centralbl. Bact. Abt. II.*, **48**: 470–500.
DITTRICH, G., 1902, Zur Entwicklungsgeschichte der Helvellineen, *Beitr. Biol. Pfl.* [Cohn], **8**: 17–52.

DITTSCHLAG, E., 1910, Zur Kenntnis der Kernverhältnisse von Puccinia Falcariae, *Centralbl. Bact. II Abt.*, **28**: 473–492, *pl. 1–3.*

DODGE, B. O., 1912, Methods of culture and the morphology of the archicarp in certain species of the Ascobolaceae, *Bull. Torrey Botan. Club*, **39**: 139–197.

———, 1914, The morphological relationship of the Florideae and the Ascomycetes, *Bull. Torrey Botan. Club*, **41**: 157–202.

———, 1918, Studies in the genus Gymnosporangium I, *Mem. Brooklyn Botan. Gard.*, **1**: 128–140.

———, 1918*a*, Studies in the genus Gymnosporangium III, *Mycologia*, **10**: 182–193.

———, 1920, The life history of Ascobolus magnificus, *Mycologia*, **12**: 115–134, *pl. 7, 8.*

———, 1922, Studies in the genus Gymnosporangium IV, *Amer. Jour. Botany*, **9**: 354–365, *pl. 22.*

———, 1922*a*, A Lachnea with a botryose conidial stage, *Bull. Torrey Botan. Club*, **49**: 301–305.

———, 1923, Morphology and host relations of Pucciniastrum americanum, *Jour. Agr. Res.*, **24**: 885–894, *pl. 1–5.*

———, 1923*a*, Origin of the central and ostiolar cavities in pycnidia of certain fungous parasites of fruits, *Jour. Agr. Res.*, **23**: 743–759, *pl. 1–6.*

———, 1923*b*, A new type of orange rusts on blackberry, *Jour Agr. Res.*, **25**: 491–494, *pl. 1.*

———, 1924, Aecidiospore discharge as related to the character of the spore wall, *Jour. Agr. Res.*, **27**: 749–756.

———, 1924*a*, Uninucleated aecidiospores in Caeoma nitens and associated phenomena, *Jour. Agr. Res.*, **28**: 1045–1058, *pl. 1–5.*

———, 1925, Organization of the telial sorus in the pine rust, Gallowaya pinicola Arth., *Jour. Agr. Res.*, **31**: 641–651, *pl. 1–2.*

———, 1927, Nuclear phenomena associated with heterothallism and homothallism in the Ascomycete Neurospora, *Jour. Agr. Res.*, **35**: 289–306, *pl. 1–3.*

DODGE, B. O., and L. O. GAISER, 1926, The question of nuclear fusions in the blackberry rust Caeoma nitens, *Jour. Agr. Res.*, **32**: 1003–1023, *pl. 1–3.*

DODGE, C. W., 1929, The higher Plectascales, *Ann. Myc.*

DOIDGE, E. M., 1920, South African Ascomycetes, *Bothalia*, **1**: 65–82.

———, 1920*a*, South African Perisporiaceae III, *Trans. R. Soc. South Africa*, **8**: 107–143.

———, 1920*b*, South African Microthyriaceae, *Trans. R. Soc. South Africa*, **8**: 235–282.

———, 1921, The haustoria of the genera Meliola and Irene, *Trans. R. Soc. South Africa*, **9**: 117–127.

DOMARADSKY, M., 1908, Zur Fruchtkörperentwicklung von Aspergillus Fischeri, *Ber. Deutsch. Botan. Ges.*, **26a**: 14–16.

DOMBROWSKI, W., 1907, Sur l'Endomyces fibuliger, *Comptes Rendus Trav. Lab. Carlsberg*, **7**: 247–266.

DOUGLAS, G. E., 1916, A study of development in the genus Cortinarius, *Amer. Jour. Botany*, **3**: 319–335, *pl. 8–13.*

———, 1918, The development of some exogenous species of agarics, *Amer. Jour. Botany*, **5**: 36–54, *pl. 1–7.*

———, 1920, Early development of Inocybe, *Botan. Gaz.*, **70**: 211–220, *pl. 18–22.*

DRECHSLER, C., 1927, Two water molds causing tomato rootlet injury, *Jour. Agr. Res.*, **34**: 287–296, *2 fig.*

DUFF, G. H., 1920, Development of the Geoglossaceae, *Botan. Gaz.*, **69**: 341–346.

———, 1922, Development of the Geoglossaceae, *Botan. Gaz.*, **74**: 264–291, *pl. 8–12.*

DURAND, E. J., 1900, The classification of the fleshy Pezizineae with reference to the structural characters illustrating the bases of their division into families, *Bull. Torrey Botan. Club*, **27**: 463–495, *pl. 27–32.*

———, 1908, The Geoglossaceae of North America, *Ann. Myc.*, **6**: 387–477, *pl. 5–22.*

EDGERTON, C. W., 1914, Plus and minus strains in the genus Glomerella, *Amer. Jour. Botany*, **1**: 244–254, *pl. 22–23.*

EDGERTON, C. W., and E. C. TIMS, 1926, Notes on Testicularia Cyperi, *Mycologia*, **18**: 169–171, *pl. 20.*

EFTIMIU, P., 1927, Contribution à l'étude cytologique des Exoascacées, *Le Botaniste*, **18**: 1–154, *3 pl. 38 fig.*

EFTIMIU, P., and S. KHARBUSH, 1927, Recherches sur les Exobasidiées, *Rev. path. vég. entomol. agric.*, **14**: 62–88, *1 pl. 9 f.*

EIDAM, E., 1876, Die Keimung der Sporen und die Entstehung der Fruchtkörper bei den Nidularieen, *Beitr. Biol. Pfl.* [Cohn], **2**: 221–248, *pl. 10.*

———, 1880, Beitrag zur Kenntniss der Gymnoasceen, *Beitr. Biol. Pfl.* [Cohn], **3**: 267–305, *pl. 12–15.*

———, 1883, Zur Kenntnis der Entwicklung bei den Ascomyceten, *Beitr. Biol. Pfl.* [Cohn], **3**: 377–433, *pl. 19–23.*

———, 1887, Basidiobolus, eine neue Gattung der Entomophthoraceen, *Beitr. Biol. Pfl.* [Cohn], **4**: 181–251, *pl. 11–12.*

ELLIOTT, J. A., 1923, The ascigerous stage of the sweet potato black-rot fungus, *Phytopathology*, **13**: 56.

———, 1925, A cytological study of Ceratostomella fimbriata (E. & H.) Elliott, *Phytopathology*, **15**: 417–422, *pl. 15–16.*

ESSIG, F. M., 1922, The morphology, development and economic aspects of Schizophyllum commune Fries, *Univ. California Pub. Botany*, **7**: 447–498, *pl. 51-61.*

ERNST, A., 1918, Bastardierung als Ursache der Apogamie im Pflanzenreich [Jena], 665 p.

FAIRCHILD, D. G., 1897, Über Kernteilung und Befruchtung bei Basidiobolus ranarum Eidam, *Jahrb. Wiss. Botanik.*, **30**: 285–296, *pl. 13–14.*

FALCK, R., 1902, Die Kultur der Oidien und ihre Rückführung in die höhere Fruchtform bei den Basidiomyceten, *Beitr. Biol. Pfl.* [Cohn], **8**: 307–344, *pl. 12–17.*

———, 1904, Die Sporenverbreitung bei den Basidiomyceten und der biologische Wert der Basidie, *Beitr. Biol. Pfl.* [Cohn], **9**: 1–82.

———, 1909, Die Lenzitesfäule des Koniferenholzes, *Hausschwammforschungen* [Möller], **3**: XIII–XXXII, 1–234, *pl. 1–7.*

———, 1912, Die Meruliusfäule des Bauholzes, *Hausschwammforschungen* [Möller], **6**: I–XVI, 1–405, *pl. 1–16.*

———, 1916–1923, Über die Sporenverbreitung bei den Ascomyceten, *Myk. Unters. u. Ber.*, **1**: 77–145; 370–403, *pl. 1–2.*

FAULL, J. H., 1905, Development of the ascus and spore formation in Ascomycetes. *Proc. Boston Soc. Nat. Hist.*, **32**: 77–114, *pl. 7–11.*

———, 1911, The cytology of the Laboulbeniales, *Ann. Botany*, **25**: 649–654.

———, 1912, The cytology of Laboulbenia chaetophora and L. Gyrinidarum, *Ann. Botany*, **26**: 325–355, *pl. 37–39.*

———, 1928, The morphology, biology and phylogeny of the Pucciniastreae [in Press].

FAVORSKII, V. I., 1910, Novyia dannyia po tsitologii i istorii razvitiia Plasmodiophora Brassicae Woron., *Zapiski Kievsk. Obshchestva Estestvoispytatelei*, **20**: 149–184, *2 pl.*

FAYOD, V., 1889, Prodrome d'une histoire naturelle des Agaricinés, *Ann. Sci. Nat. Botanique*, 7 *ser.*, **9**: 181–411.

FEDERLEY, H., 1904, Die Kopulation der Konidien bei Ustilago Tragopogoni-pratensis Pers., *Ofvers. Finska Vet. Soc. Förhandl.*, **46**[2]: 1–23, *1 fig.*

FERDINANDSEN, C., and Ö. WINGE, 1914, Studies in the genus Entorrhiza, *Dansk. Bot. Ark.*, **2**[1]: 1–13.

FINK, B,. and C. A. RICHARDS, 1915, The Ascomycetes of Ohio, *Ohio State Univ. Bull.* **19**, *Nr. 28—Ohio Biol. Survey Bull.*, **5**: 1–70.

FISCH, C., 1884, Beiträge zur Kenntnis der Chytridiaceen, *Sitzungsber. Phys. Med. Soc. Erlangen*, **16**: 29–66, *pl. 1.*

FISCHER, A., 1882, Untersuchungen über die Parasiten der Saprolegnieen, *Jahrb. Wiss. Botanik*, **13**: 286–371, *pl. 13–15.*

———, 1892, Phycomycetes. *Kryptog. Fl. Deutschl.* [Rabenhorst], I, **4**: 1–505, *74 fig.*

FISCHER, C. C. E., 1909, On the development of the fructification Armillaria mucida Schrad, *Ann. Botany*, **23**: 503–507, *pl. 35.*

FISCHER, E., 1883, Beitrag zur Kenntniss der Gattung Graphiola, *Botan. Zeitung*, **41**: 745–756; 761–773; 777–788; 793–801, *pl. 6.*

———, 1884, Zur Entwicklungsgeschichte der Gastromyceten, *Bot. Zeitung*, **42**: 432–443; 447–462; 465–475; 484–494, *pl. 7.*

———, 1886, Lycogalopsis Solmsii, *Ber. Deutsch. Botan. Ges.*, **4**: 192–197, *pl. 9.*

———, 1887, Zur Entwicklungsgeschichte der Fruchtkörper einiger Phalloideen, *Ann. Jard. Botanique Buitenzorg*, **6**: 1–51.

———, 1888, Bemerkungen über den Streckungsvorgang des Phalloideenrezeptaculums, *Mitt. Naturf. Ges. Bern*, **1887**: 142–157.

———, 1888*a*, Zur Kenntniss der Pilzgattung Cyttaria, *Botan. Zeitung*, **46**: 813–831; 842–846, *pl. 12.*

———, 1890, Beiträge zur Kenntnis exotischer Pilze, *Hedwigia*, **29**: 161–171, *pl. 3.*

———, 1891, Pachyma Cocos und ähnliche sklerotienartige Bildungen, *Hedwigia*, **30**: 61–103, 193–194, *pl. 6–13.*

———, 1891*a*, Untersuchungen zur vergleichenden Entwicklungsgeschichte und Systematik der Phalloideen, *Denkschrift Schweiz. Naturf. Ges.*, **32**: 1–103, *pl. 1–6.*

———, 1893, Neue Untersuchungen zur vergleichenden Entwicklungsgeschichte und Systematik der Phalloideen, *Denkschrift Schweiz. Naturf. Ges.*, **33**: 1–51, *pl. 1–3.*

———, 1895, Die Entwicklung der Fruchtkörper von Mutinus caninus Huds., *Ber. Deutsch. Botan. Ges.*, **13**: 128–137, *pl. 12.*

———, 1896, Über den Parallelismus der Tuberaceen und Gastromyceten, *Ber. Deutsch. Botan. Ges.*, **14**: 301–311.

———, 1897, Tuberineae, [Engler and Prantl] *Die Nat. Pfl.-fam. I*, **1**: 278–290.

———, 1898, Bemerkungen über Geopora und verwandte Hypogaeen, *Hedwigia*, **37**: 56–60.

———, 1900, Untersuchungen zur vergleichenden Entwicklungsgeschichte und Systematik der Phalloideen, *Denkschrift Schweiz. Naturf. Ges.*, **36**: 1–84, *pl. 1–6.*

———, 1900, Phallineae–Plectobasidiineae [Engler and Prantl], *Die Nat. Pfl. fam.* I, **1****: 276–346.

———, 1900, Bemerkungen über die Tuberaceengattungen Gyrocratera and Hydnotrya, *Beiblatt z. Hedwigia*, **39**: 48–51.

———, 1904, Die Uredineen der Schweiz, *Beitr. Krypt. fl. d. Schweiz*, **2**[2]: xciv, 590 p.

———, 1907, Über einige kalifornische Hypogaeen, *Ber. Deutsch. Botan. Ges.*, **25**: 372–376.

———, 1908, Morphologie der Hypogäen, *Botan. Zeitung*, **66**: 141–168, *pl. 6.*

———, 1909, Genea Thwaitesii (B. et Br.) Petch und die Verwandtschaftsverhältnisse der Gattung Genea, *Ber. Deutsch. Botan. Ges.*, **27**: 264–270, *pl. 12.*

———, 1910, Neuere Untersuchungen über die Fruchtkörperentwicklung und die Verwandtschaftsverhältnisse der Tuberineen und Helvellineen, *Zeitschr. f. Botanik*, **2**: 718–722.

———, 1910*a*, Beiträge zur Entwicklungsgeschichte der Uredineen, *Centralbl. Bact. II Abt.*, **28**: 139–152.

FISCHER, E., 1910*b*, Die Fruchtkörperentwicklung von Aseroë, *Ann. Jard. Botanique Buitenzorg, Suppl.*, **3**: 595–614, *pl. 18–19.*

———, 1910, Beiträge zur Morphologie und Systematik der Phalloideen, *Ann. Myc.*, **8**: 314–322, *pl. 5.*

———, 1912, Pilze, *Handwörterbuch der Naturwiss.*, **7**: 880–929.

———, 1919, Die Beziehungen zwischen Sexualität und Reproduktion im Pflanzenreich, *Mitt. Naturf. Ges. Bern.*, **1918**: XIX–XXI.

———, 1920, Zur Kenntnis von Graphiola und Farysia, *Ann. Myc.*, **18**: 188–197, *7 fig.*

———, 1921, Mykologische Beiträge 18–20, *Mitt. Naturf. Ges. Bern*, **1920**: 137–155.

———, 1922, Mykologische Beiträge 21–26, *Mitt. Naturf. Ges. Bern.* **1921**: 282–308.

———, 1922*a*, Weitere Beiträge zur Kenntnis der Gattung Graphiola, *Ann. Myc.*, **20**: 228–237, *4 fig.*

———, 1924, Mykologische Beiträge 27–30, *Mitt. Naturf. Ges. Bern*, **1923**: 39–60.

———, 1925, Zur Entwicklungsgeschichte der Fruchtkörper der Secotiaceen, *Veröffentl. Geobot. Inst. Rübel in Zürich.*, **3**: 571–582.

———, 1926, Mykologische Beiträge 31. Der Wirtswechsel von Sclerotinia Rhododendri, nebst Bemerkungen zur Frage der Entstehung der Heteroecie, *Mitt. Naturf. Ges. Bern.*, **1925**: 24–37.

———, 1927, Mykologische Beiträge 32. Zur Entwicklungsgeschichte der Fruchtkörper von Hymenogaster, *Mitt. Naturf. Ges. Bern.*, **1926**: 99–108.

FITZPATRICK, H. M., 1913, A comparative study of the development of the fruit body in Phallogaster, Hysterangium and Gautieria, *Ann. Myc.*, **11**: 119–149, *pl. 4–7.*

———, 1917, The development of the ascocarp of Rhizina undulata, *Botan. Gaz.*, **63**: 282–296, *pl. 27, 28.*

——— 1918, The cytology of Cronartium musciola, *Amer. Jour. Botany*, **5**: 397–419, *pl. 30–32.*

———, 1918*a*, The life-history and parasitism of Eocronartium muscicola, *Phytopathology*, **8**: 197–218, *pl. 1.*

———, 1918*b*, Sexuality in Rhizina undulata, *Botan. Gaz.*, **65**: 201–226, *pl. 3, 4.*

———, 1920, Monograph of the Coryneliaceae, *Mycologia*, **12**: 206–267, *pl. 12–18.*

———, 1923, Monograph of the Nitschkieae, *Mycologia*, **15**: 23–67, *pl. 1–7.*

FOËX, E., 1912, Les modes d'hibernation des Erysiphaceae dans la région de Montpellier, *Congrès internat. de pathologie comparée*, 6 p.

———, 1912, Miscellanées, *Ann. Ecole Nat. Agr. Montpellier 2 sér.*, **11**: 3–21, *pl. 6.*

———, 1913, Evolution du conidiophore de Sphaerotheca Humuli, *Bull. Soc. Myc. France*, **29**: 251–252, *pl. 10.*

———, 1913, Recherches sur Oidiopsis taurica. *Bull. Soc. Myc. France*, **29**: 577–588, *pl. 35–38.*

FRASER, H. C. I., 1907, On the sexuality and development of the ascocarp in Lachnea stercorea, *Ann. Botany*, **21**: 349–360, *pl. 29, 30.*

———, 1907, Contributions to the cytology of Humaria rutilans, *Ann. Botany*, **21**: 307–308.

———, 1908, Contributions to the cytology of Humaria rutilans, *Ann. Botany*, **22**: 35–55, *pl. 4, 5.*

———, 1913, The development of the ascocarp in Lachnea cretea, *Ann. Botany*, **27**: 553–563, *pl. 42, 43.*

[FRASER] GWYNNE-VAUGHAN, H. [C. I.], 1922, Fungi, Cambridge, 232 p.

FRASER, H. C. I. and S. W. ST. JOHN BROOKS, 1909, Further studies on the cytology of the Ascus, *Ann. Botany*, **23**: 537–549, *pl. 39–40.*

FRASER, H. C. I. and H. S. CHAMBERS, 1907, The morphology of Aspergillus herbariorum, *Ann. Myc.*, **5**: 419–431, *pl. 11, 12.*

FRASER, H. C. I. and E. J. WELSFORD, 1908, Further contributions to the cytology of the Ascomycetes, *Ann. Botany*, **22**: 465–477, *pl. 26, 27.*

[FRASER] GWYNNE-VAUGHAN, H. C. I. and H. S. WILLIAMSON, 1927, Germination in Lachnea cretea, *Ann. Botany*, **41**: 489–495, *3 fig.*

FREEMAN, D. L., 1910, Untersuchungen über die Stromabildung der Xylaria Hypoxylon in künstlichen Kulturen, *Ann. Myc.*, **8**: 192–211, *pl. 4.*

FREY, C. N., 1924, The cytology and physiology of Venturia inaequalis (Cooke) Winter, *Trans. Wisconsin Acad. Sci*, **21**: 303–341, *pl. 10–11.*

FRIES, R. E., 1899, Basidiobolus myxophilus en ny Phycomycet, *Bih. Svenska Vet. Akad. Handl.*, **25**, *Afd.* III, *no.* 3: 1–16, *pl. 1–2.*

———, 1910, Om utvecklingen af fruchtkroppen och peridiolerna hos Nidularia, *Svensk. Botan. Tidskr.*, **4**: 126–138, *pl. 5.*

———, 1911, Über die cytologischen Verhältnisse bei der Sporenbildung von Nidularia, *Zeitschr. f. Botanik*, **3**: 145–165, *pl. 1, 2.*

———, 1911, Zur Kenntnis der Cytologie von Hygrophorus conicus, *Svensk Botan. Tidskr.*, **5**: 241–251, *pl. 1.*

FROMME, F. D., 1912, Sexual fusions and spore development of the flax rust, *Bull. Torrey Botan. Club*, **39**: 113–131, *pl. 8, 9.*

———, 1914, The morphology and cytology of the aecidium cup, *Botan. Gaz.*, **58**: 1–35, *pl. 1, 2.*

FRON, G., and A. GAILLAT, 1925, Contribution à l'étude du genre Ligniera, *Bull. Soc. Myc. France*, **41**: 388–390, *pl. 10.*

FUCHS, J., 1913, Beitrag zur Kenntnis der Pleonectria berolinensis, *Arb. K. Biol. Anst. Land- u. Forstw.*, **9**: 324–332.

FÜNFSTÜCK, M., 1902, Der gegenwärtige Stand der Flechtenforschung nebst Ausblicken auf deren voraussichtliche Weiterentwickelung, *Ber. Deutsch. Botan. Ges.*, **20**: 62–77.

FUISTING, W., 1867, Zur Entwicklungsgeschichte der Pyrenomyceten, *Botan. Zeitung*, **25**: 177–181, 185–189, 193–198.

———, 1868, Zur Entwicklungsgeschichte der Pyrenomyceten II, *Botan. Zeitung*, **26**: 369–375; 385–398; 401–407; 417–422, *pl. 7.*

FULTON, T. W., 1889, The dispersion of the spores of fungi by the agency of insects, with special reference to the Phalloidei, *Ann. Botany*, **3**: 207–238, *pl. 15.*

GÄUMANN, E., 1918, Ein Beitrag zur Kenntnis der lappländischen Saprolegnieen, *Botan. Notiser*, **1918**: 151–159.

———, 1918*a*, Über die Formen der Peronospora parasitica, (Pers.) Fries, *Beih. Botan. Centralbl.* 1 *Abt.*, **35**: 1–143; 395–533.

———, 1922, Über die Gattung Kordyana, *Ann. Myc.*, **20**: 257–271.

———, 1922*a*, Über das Septobasidium bogoriense, *Ann. Myc.*, **20**: 160–173, *pl. 2.*

———, 1922*b*, Über die Entwicklungsgeschichte von Iola javensis, *Ann. Myc.*, **20**: 272–289, *pl. 3.*

———, 1922*c*, Uber die Entwicklungsgeschichte von Lanomyces, *Ann. Jard. Botanique Buitenzorg*, **32**: 43–63.

———, 1923, Beiträge zu einer Monographie der Gattung Peronospora, *Beitr. Krypt. fl. der Schweiz.*, **5**[4]: 1–360.

———, 1926, Vergleichende Morphologie der Pilze, 626 p. Jena.

———, 1927, Mykologische Mitteilungen III, 1. Uber die Entwickelungsgeschichte von Epichloe bambusae Pat. 2. Uber die Gattung Woroninella Rac., *Ann. Myc.*, **25**: 167–174.

GAILLARD, A., 1892, Le genre Meliola, *Thèse* [Paris], 163 p., *24 pl.*

GALLAUD, J., 1905, Études sur une Entomophthorée saprophyte, *Ann. Sci. Nat. Botanique, IX*, **1**: 101–134.

GASSNER, G., 1916, Untersuchungen über die Abhängigkeit des Auftretens der Getreideroste vom Entwicklungszustand der Nährpflanze und von äusseren Faktoren, *Centralbl. Bact. II*, **44**: 512–617.

GIESENHAGEN, K., 1895, Die Entwicklungsreihen der parasitischen Exoasceen, *Flora*, **81**: 267–361.

———, 1901, Taphrina, Exoascus und Magnusiella, *Botan. Zeitung*, **59**[1]: 115–142.

GILBERT, A. H., and C. W. BENNETT, 1917, Sclerotinia trifoliorum, the cause of stem rot of clovers and alfalfa, *Phytopathology*, **7**: 432–442, *f. 1–5*.

GILBERT, E. M., 1921, Cytological studies of the lower Basidiomycetes. I. Dacrymyces, *Trans. Wisconsin Acad. Sci.*, **20**: 387–397, *pl. 29*.

GILBERT, J., 1918, Le genre Amanita, *Thèse pharm.* [Paris], 186 p.

GILKEY, H. M., 1916, A revision of the Tuberales of California, *Univ. California Publ. Botany*, **6**: 275–356, *pl. 27–30*.

GJURAŠIN, S., 1925, Mycogalopsis retinospora nov. gen. et nov. spec. et son développement, *Acta Bot. Inst. Botan. R. Univ. Zagreb.*, **1**: 1–14, *10 fig.*

GOEBEL, K., 1902, Die verschiedene Ausbildung der Fruchtkörper von Stereum hirsutum, *Flora*, **90**: 471–476.

GOELDI, E. A., and E. FISCHER, 1917, Der Generationswechsel im Tier- und Pflanzenreich mit Vorschlägen zu einer einheitlichen biologischen Auffassung und Benennungsweise, *Mitt. Naturf. Ges. Bern*, **1916**: 60–111, *3 pl.*

GOLDSTEIN, B., 1923, Resting spores of Empusa Muscae, *Bull. Torrey Botan. Club*, **50**: 317–327, *pl. 19*.

GREEN, E., 1927, The life history of Zygorhynchus Moelleri Vuill., *Ann. Botany*, **41**: 419–435, *10 fig.*

GRIFFITHS, D., 1901, The North American Sordariaceae, *Mem. Torrey Botan. Club*, **11**: 1–134, *pl. 1–19*.

GRIFFITHS, D., and F. J. SEAVER, 1910, Fimetariaceae, *N. Amer. Fl.*, **3**: 65–88.

GRIGGS, R. F., 1909, Mitosis in Synchytrium with some observations on the individuality of chromosomes, *Botan. Gaz.*, **48**: 339–358, *pl. 16–18*.

———, 1909, Some aspects of amitosis in Synchytrium, *Botan. Gaz.*, **47**: 127–138, *pl. 3–4*.

———, 1910, Monochytrium, a new genus of the Chytridiales, its life history and cytology, *Ohio Naturalist*, **10**: 44–54.

———, 1912, The development and cytology of Rhodochytrium, *Botan. Gaz.*, **53**: 127–173, *pl. 11–16*.

GRIGORAKI, L., 1925, Recherches cytologiques et taxonomiques sur les dermatophytes et quelques autres champignons parasites, *Ann. Sci. Nat. Botanique, ser. 10*, **7**: 165–444, *pl. 1–28*.

GROSSENBACHER, J. G., and B. M. DUGGAR, 1911, A contribution to the life-history, parasitism and biology of Botryosphaeria Ribis, *New York Agr. Exp. Sta. Techn. Bull.*, **18**: 115–190.

GROVE, W. B., 1913, The evolution of the higher Uredineae, *New Phytologist*, **12**: 89–106.

GRUBER, E., 1912, Einige Beobachtungen über den Befruchtungsvorgang bei Zygorhynchus Moelleri Vuill., *Ber. Deutsch. Botan. Ges.*, **30**: 126–133, *pl. 4*.

GÜSSOW, H. T., 1912, Der Milchglanz der Obstbäume, *Zeitschr. f. Pflanzenkrank.*, **22**: 385–401, *pl. 5–6*.

GUILLIERMOND, A., 1902, Recherches cytologiques sur les levures et quelques moissures à formes levures, *Thèse* [Paris], 289 p.

———, 1903, Recherches cytologiques sur les levures, *Rev. Gén. Bot.*, **15**: 49–66; 104–124; 166–185, *pl. 1–9*.

———, 1903*a*, Contribution à l'étude de l'épiplasme des Ascomycètes et recherches sur les corpuscules metachromatiques des champignons, *Ann. Myc.* **1**: 201–215, *pl. 6, 7*.

———, 1903*b*, Recherches sur la germination des spores dans le Saccharomyces Ludwigii, *Bull. Soc. Myc., France*, **19**: 19–32, *pl. 1*.

GUILLIERMOND, A., 1904, Contribution à l'étude de la formation des asques et de l'épiplasme des Ascomycètes, *Rev. Gén. Botanique*, **16**: 49–65, *pl. 8, 9.*

———, 1904*a*, Sur le noyau de la levure, *Ann. Myc.*, **2**: 184–189.

———, 1904*b*, Recherches sur la karyokinese chez les Ascomycètes, *Rev. Gén. Botanique*, **16**: 129–143, *pl. 14–15.*

———, 1905, Recherches sur la germination des spores et la conjugaison chez les levures, *Rev. Gén. Botanique*, **17**: 337–376, *pl. 6–9.*

———, 1905*a*, Remarques sur la karyokinèse des Ascomycètes, *Ann. Myc.*, **3**: 343–361, *pl. 10–12.*

———, 1907, A propos de l'origine des levures, *Ann. Myc.*, **5**: 49–69.

———, 1908, La question de la sexualité chez les Ascomycètes, *Rev. én. Botanique*, **20**: 32–39; 85–89; 111–120; 178–182; 298–305; 332–344; 364–378.

———, 1909, Recherches cytologiques et taxonomiques sur les Endomycétacées, *Rev. Gén. Botanique*, **21**: 353–391; 401–419, *pl. 12–19.*

———, 1909*a*, Sur la phylogenèse des levures, *Comptes Rendus Hebd. Soc. Biol. Paris*, **66**: 998–1000.

———, 1910, Remarques critiques sur différentes publications sur la cytologie des levures et quelques observations sur la structure de ces champignons, *Centralbl. Bact. II Abt.*, **26**: 577–589.

———, 1910*a*, Quelques remarques sur la copulation des levures, *Ann. Myc.*, **8**: 287–297.

———, 1910*b*, Remarques sur Endomyces fibuliger, *Comptes Rendus Hebd. Soc. Biol. Paris*, **68**: 318– 320.

———, 1911, Aperçu sur l'évolution nucléaire des Ascomycètes, *Rev. Gén. Botanique*, **23**: 89–120, *pl.* 4–5.

———, 1911*a*, Sur un exemple de copulation hétérogamique observé chex une levure, *Comptes Rendus Hebd. Soc. Biol. Paris*, **70**: 442–444.

———, 1912, Les levures [Paris, Doin], 565 p.

———, 1912*a*, Nouvelles observations sur la sexualité des levures, *Arch. f. Protistenk.*, **28**: 52–77, *pl. 6–9.*

———, 1913, Les progrès de la cytologie des champignons, *Prog. Rei botan.*, **4**: 389–542.

———, 1913*a*, Recherches comparatives sur le développement de l'Endomyces fibuliger, et de l'E. capsularis et nouvelles remarques sur la signification des anastomoses qui se produise dans l'E. fibuliger, *Livre jubilaire van Laer* [Gand], 36–71.

———, 1914, Monographie des levures rapportées d'Afrique occidentale, *Ann. Sci. Nat. Bot. IX*, **19**: 1–32, *pl. 1–5.*

———, 1917, Sur la division nucléaire des levures, *Ann. Inst. Pasteur*, **31**: 107–113, *pl. 4.*

———, 1918, Zygosaccharomyces Nadsonii nouvelle espèce de levures à conjugaison hétérogamique, *Bull. Soc. Myc. France*, **34**: 111–122, *pl. 7.*

———, 1919, Sur une nouvelle levure à copulation hétérogamique, *Comptes Rendus Hebd. Soc. Biol. Paris*, **82**: 466–470.

———, 1920, Zygosaccharomyces Pastorii, nouvelle espèce de levures à copulation hétérogamique, *Bull. Soc. Myc. France*, **36**: 203–211, *pl. 11–13.*

GUILLIERMOND, A. and G. PÉJU, 1919, Sur un nouveau champignon présentant des caractères intermédiares entre les levures et les Endomyces, *Comptes Rendus Hebd. Soc. Biol. Paris*, **82**: 1343–1346.

———, 1920, Une nouvelle espéce de levure, Debaryomyces, D. Kloeckerii n. sp., *Bull. Soc. Myc. France*, **36**: 164–171, *pl. 6–10.*

———, 1921, Une nouvelle espéce de levure du genre Debaryomyces, *Bull. Soc. Myc. France*, **37**: 35–38.

GUILLIERMOND, A. and F. J. TANNER, 1920, The yeasts, Wiley & Sons [New York], 424 p.

GUSEVA, K. A., 1923, K istorii razvitiia Fabraea Ranunculi Karsten, *Trav. Sect. Mycol. Phytopath., Soc. Bot. Russ.*, [in Russian] **1**: 39–45, *pl. 4.*

GUYOT, A. L., 1927, Quelques observations sur les Ligniera radicicoles, *Rév. Path. Veg. Entomol. Agr.*, **14**: 176–183, *3 fig.*

GWYNNE-VAUGHAN, H. C. I. [FRASER], see [Fraser] Gwynne-Vaughan, H. C. I.

HAACK, O., 1911, Der Schüttepilze der Kiefer, *Zeitschr. f. Forst.- und Jadgwesen*, **43**: 329–357, 402–423, 481–505, *2 pl.*

HAENICKE, A., 1916, Vererbungsphysiologische Untersuchungen an Arten von Penicillium, *Zeitschr. f. Botanik*, **8**: 225–343.

HAGEM, O., 1908, Untersuchungen über norwegische Mucorineen I, [Christiania] *Vid. Selsk. Skrift., I. Math. Naturv. Kl.*, **1907**[7]: 1–50.

———, 1910, Untersuchungen über norwegische Mucorineen II, [Christiania] *Vid. Selsk. Skrift. I. Math. Naturv. Kl.*, **1910**[4]: 1–152.

HANNA, W. F., 1925, The problem of sex in Coprinus lagopus, *Ann. Botany*, **39**: 431–457.

HARIOT, P., 1908 Les urédinées, [Paris] 378 p.

HARKNESS, H. W., 1899, Californian hypogaeous fungi, *Proc. Calif. Acad. Sci. III. Botany*, **1**: 241–292, *pl. 42–45.*

HARPER, R. A., 1895, Die Entwicklung des Peritheciums bei Sphaerotheca Castagnei, *Ber. Deutsch. Botan. Ges.*, **13**: 475–481, *pl. 39.*

———, 1896, Über das Verhalten der Kerne bei der Fruchtentwicklung einiger Ascomyceten, *Jahrb. Wiss. Botanik*, **29**: 655–685, *pl. 11, 12.*

———, 1897, Kernteilung und freie Zellbindung im Ascus, *Jahrb. Wiss. Botanik*, **30**: 249–284, *pl. 11, 12.*

———, 1898, Nuclear phenomena in certain stages in the development of the smuts, *Trans. Wisconsin Acad. Sci.*, **12**: 475–498, *pl. 8–9.*

———, 1899, Cell division in sporangia and asci, *Ann. Botany*, **13**: 467–525, *pl. 24–26.*

———, 1900, Sexual reproduction in Pyronema confluens and the morphology of the ascocarp, *Ann. Botany*, **14**: 321–400, *pl. 19–21.*

———, 1902, Binucleate cells in certain Hymenomycetes, *Botan. Gaz.*, **33**: 1–25, *pl. 1.*

———,1905, Sexual reproduction and the organization of the nucleus in certain mildews, *Carnegie Inst. Washington, Publ.*, **37**: 104 p., *7 pl.*

HARTMANN, M., 1909, Autogamie bei Protisten und ihre Bedeutung für das Befruchtungsproblem, *Arch. f. Protistenk.*, **14**: 264–334.

———, 1918, Theoretische Bedeutung und Terminologie der Vererbungserscheinungen bei haploiden Organismen, *Zeitschr. f. Ind. Abst. u. Vererb.*, **20**: 1–26.

HARVEY, J. V., 1925, A study of the water molds and Pythiums occurring in the soils of Chapel Hill, *Jour. Elisha Mitchell Sci. Soc.*, **41**: 151–164, *pl. 12–19.*

HEALD, F. D., 1913, The symptoms of chestnut tree blight and a brief description of the blight fungus, *Pennsylvania Chestnut Tree Blight Commission Bull.*, **5**: 15 p., 16 *pl.*

HEALD, F. D., and R. A. STUDHALTER, 1915, Longevity of pycnospores and ascospores of Endothia parasitica under artificial conditions, *Phytopathology*, **5**: 35–43, *pl. 2.*

HEALD, F. D., and R. C. WALTON, 1914, The expulsion of ascospores from the perithecia of the chestnut blight fungus, Endothia parasitica, *Amer. Jour. Botany*, **1**: 499–521.

HEALD, F. D., and F. A. WOLF, 1910, The structure and relationship of Urnula geaster, *Botan. Gaz.*, **49**: 182–188, *pl. 12.*

HEIN, I., 1927, Studies on morphogenesis and development of the ascocarp of Sphaerotheca Castagnei, *Bull. Torrey Botan. Club.*, **54**: 383–417, *pl. 28, 29.*

HENNINGS, P., 1901, Fungi japonici, *Botan. Jahrb.* [Engler], **28**: 259–280.

HESSE, R., 1891, Die Hypogaeen Deutschlands, [Halle a. S.,] **1**: 133 p., *pl. 1–11;* [1894], **2**: 140 p., *pl. 12–22.*

HIGGINS, B. B., 1914, Contributions to the life history and physiology of Cylindrosporium on stone fruits, *Amer. Jour. Botany,* **1**: 145–173, *pl. 13–16.*

———, 1914*a*, Life history of a new species of Sphaerella, *Myc. Centralbl.*, **4**: 187–193.

———, 1920, Morphology and life history of some Ascomycetes, *Amer. Jour. Botany,* **7**: 435–444, *pl. 30.*

HILS, E., 1912, Ursachen der Myzelbildung bei Ustilago Jensenii Rostr., *Inaug. Diss.* Tübingen, 42 p. *10 fig.*

HIMMELBAUR, W., 1911, Zur Kenntnis der Phytophthoreen, *Jahrb. Hamburg Wiss. Anst.*, **28**: 3 *Beih.*: 39–61.

HIRMER, M., 1920, Zur Kenntnis der Vielkernigkeit der Autobasidiomyceten, *Zeitschr. f. Botanik,* **12**: 657–674.

HODGETTS, W. J., 1917, On the forcible discharge of spores of Leptosphaeria acuta, *New Phytologist,* **16**: 139–146.

HÖHNEL, F. VON, 1907, Fragmente zur Mykologie III, *Sitzungsber. Akad. Wiss, Wien, Math. Nat. Kl. I Abt.*, **116**: 83–162.

———, 1909, Fragmente zur Mykologie VI, *Sitzungsber. K. Akad. Wiss. Wien, Math. Nat. Kl. I Abt.*, **118**: 275–452.

———, 1910, Atichia Treubii, *Ann. Jard. Botanique Buitenzorg Suppl.*, **3**: 19–28.

———, 1917, Über die Trichothyriaceen, *Ber. Deutsch. Botan. Ges.*, **35**: 411–416.

———, 1917, System der Phacidiales, *Ber. Deutsch. Botan. Ges.*, **35**: 416–422.

———, 1917, Über die Perithecien der Microthyriaceen und die Gattung Meliola Fries, *Ber. Deutsch. Botan. Ges.*, **35**: 698–702.

———, 1918, Mykologische Fragmente, *Ann. Myc.*, **16**: 35–174.

———, 1918, Über die Gattung Leptosphaeria, *Ber. Deutsch. Botan. Ges.*, **36**: 135–140.

———, 1918, Über den Zusammenhang von Meliola mit den Microthyriaceen, *Ber. Deutsch. Botan. Ges.*, **36**: 471–473.

———, 1920, Über Pseudopeziza, Pyrenopeziza, Ephelina und Spilopodia, *Ber. Deutsch. Botan. Ges.*, **38**: 96–101.

———, 1923, System der Fungi imperfecti, *Myk. Unters. u. Ber.* [Falck], **1**: 301–403.

HÖHNEL, F. VON and V. LITSCHAUER, 1906, Revision der Corticieen in Dr. J. Schröters "Pilze Schlesiens" nach seinen Herbarexemplaren, *Ann. Myc.*, **4**: 288–294.

———, 1906, Beiträge zur Kenntnis der Corticieen, *Sitzungsber. K. Akad. Wiss. Wien. Math. Naturw. Kl. I Abt.*, **115**: 1549–1620.

———, 1907, II *Ibid.*, **116**: 739–852, *pl. 1–4.*

———, 1908, III *Ibid.*, **117**: 1081–1124.

HOFFMANN, A. W. H., 1912, Zur Entwicklungsgeschichte von Endophyllum Sempervivi, *Centralbl. Bact. II Abt.*, **32**: 137–158, *pl. 1–2.*

HOLDEN, R. J. and R. A. HARPER, 1902, Nuclear divisions and nuclear fusions in Coleosporium Sonchi-arvensis Lev., *Trans. Wisconsin Acad. Sci.*, **14**: 63–82, *pl. 1–2.*

HOLLOS, L., 1904, Die Gastromyceten Ungarns, Leipzig, 278 p., *29 pl.*

HORI, S., 1907, On Ustilago esculenta P. Henn., *Ann. Myc.*, **5**: 150–154, *pl. 6–7.*

HOTSON, J. W., 1912, Culture studies of fungi producing bulbils and similar propagative bodies, *Proc. Amer. Acad. Arts Sci.*, **48**: 227–306, *pl. 1–12.*

HUMPHREY, J. E., 1892, The Saprolegniaceae of the United States, *Trans. Amer. Phil. Soc.*, **17**: 63–148.

HUNTER, L. M., 1927, Comparative study of spermogonia of rusts of Abies, *Botan. Gaz.*, **83**: 1–23, *pl. 1–4.*

IKENO, S., 1903, Über die Sporenbildung und systematische Stellung von Monascus purpureus, *Ber. Deutsch. Botan. Ges.*, **21**: 259–269, *pl. 13.*

———, 1903*a*, Die Sporenbildung von Taphrinaarten, *Flora,* **92**: 1–31, *pl. 1–3.*

ISTVANFFI, G. VON, 1895, Über die Rolle der Zellkerne bei der Entwicklung der Pilze, *Ber. Deutsch. Botan. Ges.*, **13**: 452–467, *pl. 35–37.*

———, 1896, Untersuchungen über die physiologische Anatomie der Pilze, *Jahrb. Wiss. Botanik.*, **29**: 391–440, *pl. 3–7.*

ISTVANFFI, G. VON and O. JOHAN-OLSEN, 1887, Über die Milchsaftbehälter und verwandte Bildungen bei den höheren Pilzen, *Botan. Centralbl.*, **29**: 372–375, 385–390.

ISTVANFFI, G. VON and G. PALINKAS, 1913, Études sur le mildiou de la vigne, *Ann., Inst. Centr. Ampélolog. R. Hongrois.*, **4**: 1–125, *pl. 1–9.*

ITO, S., 1915, On Typhulochaeta, a new genus of Erysiphaceae, *Botan. Mag. Tokyo*, **29**: 15–22, *pl. 1.*

IWANOFF, B., 1907, Untersuchungen über den Einfluss des Standortes auf den Entwickelungsgang und den Peridienbau der Uredineen, *Centralbl. Bact. II*, **18**: 265–288; 470–480; 655–672.

JACZEWSKI, A. DE, 1894, Essai de classification naturelle des Pyrénomycètes, *Bull. Soc. Myc. France*, **10**: 13–48.

———, 1910, Studien über das Verhalten des Schwarzrostes des Getreides in Russland, *Zeitschr. Pflanzenkrankh.*, **20**: 321–359.

JANCHEN, E., 1923, Die Stellung der Uredineen und Ustilagineen im System der Pilze, *Österr. Botan. Zeitschr.*, **72**: 164–180, *pl. 4*; 302–304, *pl. 11.*

JOHNSTON, J. R., 1903, On Cauloglossum transversarium Fr., *Proc. Amer. Acad. Arts Sci.*, **38**: 61–74. *1 pl.*

JOLIVETTE, H. D. M., 1910, Spore formation in Gleoglossum glabrum, *Trans. Wisconsin Acad. Sci.*, **16**: 1171–1190.

JOLIVETTE-SAX, H. [D. M.], 1918, Spore formation in Philocopra coeruleotecta, *Amer. Jour. Botany*, **5**: 61–78, *pl. 9–11.*

JOHOW, F., 1884, Die Gruppe der Hymenolichenen, *Jahrb. Wiss. Botanik*, **15**: 361–409, *pl. 17–21.*

JONES, F. R. and C. DRECHSLER, 1920, Crownwart of alfalfa caused by Urophylyctis alfalfae, *Jour. Agr. Res.*, **20**: 295–323, *pl. 47–56.*

———, 1925, Root rot of peas in the United States caused by Aphanomyces euteiches (n. sp.), *Jour. Agr. Res.*, **30**: 293–325.

JONES, S. G., 1923, Life history of Rhytisma acerinum, *Ann. Botany*, **37**: 731–732.

———, 1925, Life history and cytology of Rhytisma acerinum, *Ann. Botany*, **39**: 41–75, *pl. 4.*

———, 1926, The development of the perithecium of Ophiobolus graminis Sacc., *Ann. Botany*, **40**: 607–629, *pl. 18–19.*

JUEL, H. O., 1895, Hemigaster, ein neuer Typus unter den Basidiomyceten, *Bih. Svenska Vet. Akad. Handl.*, **21**: *Afd. III, Nr. 4:* 1–22.

———, 1897, Muciporus und die Familie der Tulasnellaceen, *Bih. Svenska Vet. Akad. Handl.*, **23**, *Afd. III, Nr. 12:* 1–27, *1 pl.*

———, 1898, Die Kernteilungen in den Basidien und die Phylogenie der Basidiomyceten, *Jahrb. Wiss. Botanik*, **32**: 361–388, *pl. 4.*

———, 1898, Stilbum vulgare Tode. Ein bisher verkannter Basidiomycet, *Bih. Svenska. Vet. Akad. Handl.*, **24**, *Afd. III, Nr. 9:* 1–15, *1 pl.*

———, 1901, Pyrrhosorus, eine neue marine Pilzgattung, *Bih. Svenska Vet. Akad. Handl.*, **26**, *Afd. III. Nr. 14:* 1–16, *1 pl.*

———, 1902, Über Zellinhalt, Befruchtung und Sporenbildung bei Dipodascus, *Flora*, **91**: 47–55, *pl. 7–8.*

———, 1909, Om Taphrina-arter på Betula, *Svensk Bot. Tidskr.*, **3**: 183–191, *pl. 6–8.*

———, 1912, Beiträge zur Kenntnis der Gattungen Taphrina und Exobasidium, *Svensk Bot. Tidskr.*, **6**: 353–372, *pl. 7.*

JUEL, H. O., 1915, Berichtigung über die Gattung Muciporus, *Ark. f. Botanik*, **14**[1]: 1–9, *pl. 1.*

———, 1916, Cytologische Pilzstudien I, Die Basidien der Gattungen Cantharellus, Craterellus und Clavaria, *Nova Acta R. Soc. Sci. Upsal.*, IV, **4**[6]: 1–36, *pl. 1–3.*

———, 1921, Cytologische Pilzstudien II, Zur Kenntnis einiger Hemiasceen, *Nova Acta R. Soc. Sci. Upsal.*, IV, **5**[5]: 1–43, *2 pl.*

KANOUSE, B. B., 1925, Physiology and morphology of Pythiomorpha gonapodioides, *Botan. Gaz.*, **79**: 196–206, *pl. 12–13.*

———, 1927, A monographic study of special groups of water molds. I. Blastocladiaceae, *Amer. Jour. Botany*, **14**: 287–306, *pl. 32–34.* II. Leptomitaceae and Pythiomorphaceae. *Ibid.*, **14**: 335–357, *pl. 48.*

KASANOVSKY, V., 1911, Aphanomyces laevis deBy., *Ber. Deutsch. Botan .Ges.*, **29**: 210–228, *pl. 10.*

KAUFFMAN, C. H., 1908, Contribution to the physiology of the Saprolegniaceae, with special reference to the variations of the sexual organs, *Ann. Botany*, **22**: 361–387, *pl. 23.*

———, 1921, Isoachlya, a new genus of the Saprolegniaceae, *Amer. Journ. Botany*, **8**: 231–237, *pl. 13–14.*

KEENE, M. L., 1914, Cytological studies of the zygospores of Sporodinia grandis, *Ann. Botany*, **28**: 455–470, *pl. 35, 36.*

KEMPTON, F. E., 1919, Origin and development of the pycnidium, *Botan. Gaz.*, **68**: 233–261, *pl. 17–22.*

KHARBUSH, S., 1927, Évolution nucleaire du Sclerotinia Fuckeliana deBary, *Bull. Soc. Bot. France*, **74**: 257–262, *1 fig.*

KIHLMAN, O., 1883, Zur Entwicklungsgeschichte der Ascomyceten, [Helsingfors] 43 p., *pl. 1–2* [preprinted from *Acta Soc. Sci. Fenn.*, **14**: 309–351, *2 pl.*]

KILLIAN, C., 1917. Uber die Sexualität von Venturia inaequalis. *Zeitschr. f. Botanik*, **9**: 353–398.

———, 1918, Morphologie Biologie und Entwicklungsgeschichte von Cryptomyces Pteridis (Rebent.) Rehm, *Zeitschr. f. Botanik*, **10**: 49–126.

———, 1919, Sur la sexualité de l'ergot de seigle, le Claviceps purpurea (Tulasne), *Bull. Soc. Myc. France*, **35**: 182–197, *pl. 10–17.*

———, 1920, Le développement du Dothidella Ulmi, *Rev. Gén. Botanique*, **32**: 534–551, *pl. 16–19.*

———, 1921, La sexualité des Ascomycètes, *Bull. Biol. France Belg.*, **54**: 179–251.

———, 1922, Le développement du Stigmatea Robertiani, *Rev. Gén. Botanique*, **34**: 577–589, *pl. 14–17.*

———, 1924, Le développement du Graphiola Phoenicis, et ses affinités, *Rev. Gén. Botanique*, **36**: 385–394; 451–460, *pl. 7–8.*

KILLIAN C. and V. LIKHITÉ, 1923, Le développement du Hendersonia foliorum, *Comptes rendus Acad. Sci.* [Paris], **177**: 484–486.

KING, C. A., 1903, Observations on the cytology of Araiospora pulchra, *Proc. Boston Soc. Nat. Hist.*, **31**: 211–245, *pl. 11–15.*

KIRBY, R. S., 1923, Heterothallism in Ophiobolus cariceti, *Phytopathology*, **13**: 35.

———, 1924, The take-all disease of cereals and grasses caused by Ophiobolus cariceti (Berkeley and Broome) Saccardo, *Mem. Cornell Univ. Agr. Exp. Sta.*, **88**: 1–45.

KLEBAHN, H., 1904, Die wirtwechselnden Rostpilze, Berlin, 477 p.

———, 1905, Untersuchungen über einige Fungi imperfecti und die zugehörigen Ascomycetenformen, I, II, *Jahrb. wiss. Botanik*, **41**: 486–560.

———, 1906, Untersuchungen über einige Fungi imperfecti und die zugehörigen Ascomycetenformen, III, *Zeitschr. f. Pflanzenkrankh.*, **16**: 65–83, *pl. 3, 4.*

———, 1907, Untersuchungen über einige Fungi imperfecti und die zugehörigen Ascomycetenformen, IV, *Zeitschr. f. Pflanzenkrankh.*, **17**: 223–237, *pl. 8.*

KLEBAHN, H., 1908, Untersuchungen über einige Fungi imperfecti und die zugehörigen Ascomycetenformen V, *Zeitschr. f. Pflanzenkrankh.*, **18**: 5–17, *pl. 3.*

——, 1908, Untersuchungen über einige Fungi imperfecti und die zugehörigen Ascomycetenformen, VI, VII, *Zeitschr. f. Pflanzenkrankh.*, **18**: 129–154, *pl. 4, 5.*

———, 1914, Kulturversuche mit Rostpilzen, *Zeitschr. f. Pflanzenkrankh.*, **24**: 1–32.

———, 1916, Kulturversuche mit Rostpilzen, *Zeitschr. f. Pflanzenkrankh.*, **26**: 257–277.

———, 1918, Haupt- und Nebenfruchtformen der Ascomyceten [Leipzig], **1**: 395 p.

———, 1924, Fabraea Fragariae, die Schlauchfruchtform der Marssonina Fragariae, *Ber. Deutsch. Botan. Ges.*, **42**: 191–197.

KLEBS, G., 1899, Zur Physiologie der Fortpflanzung einiger Pilze, *Jahrb. Wiss. Botanik*, **33**: 513–593.

KNIEP, H., 1911, Über das Auftreten von Basidien im einkernigen Myzel von Armillaria mellea, *Zeitschr. f. Botanik*, **3**: 529–553, *pl. 3–4.*

———, 1913, Beiträge zur Kenntnis der Hymenomyceten I, II, *Zeitschr. f. Botanik*, **5**: 593–637, *pl. 2–5.*

———, 1915, Beiträge zur Kenntnis der Hymenomyceten III, *Zeitschr. f. Botanik*, **7**: 369–398, *pl. 2.*

———, 1917, Beiträge zur Kenntnis der Hymenomyceten V, *Zeitschr. f. Botanik*, **9**: 81–118.

———, 1918, Über die Bedingungen der Schnallenbildung bei den Basidiomyceten, *Flora*, **111–112**: 380–395.

———, 1919, Untersuchungen über den Antherenbrand (Ustilago violacea Pers.), Ein Beitrag zum Sexualitätsproblem, *Zeitschr. f. Botanik*, **11**: 257–284.

———, 1920, Über morphologische und physiologische Geschlechtsdifferenzierung [Untersuchungen an Basidiomyzeten], *Verh. Phys. Med. Ges. Würzburg, N. F.*, **46**: 1–18.

———, 1921, Über Urocystis Anemones (Pers.) Winter, *Zeitschr. f. Botanik*, **13**: 289–311, *pl. 3.*

———, 1922, Über Geschlechtsbestimmung und Reduktionsteilung, *Verh. Phys. Med. Ges. Würzburg, N. F.*, **47**: 1–29.

———, 1923, Über erbliche Änderungen von Geschlechtsfaktoren bei Pilzen, *Zeitschr. Ind. Abstammungs- und Vererb.*, **31**: 170–183.

———, 1926, Über Artkreuzung bei Brandpilzen, *Zeitsch. f. Pilzk.*, **10**: 217–248.

KNOLL, F., 1912, Untersuchungen über den Bau und die Funktionen der Cystiden und verwandter Organe, *Jahrb. Wiss. Botanik*, **50**: 453–501.

KOHN, F. G., 1908, Die Hefepilze [Leipzig], 343 p.

KOMARNITZKY, N., 1914, Über die Sporenbildung bei Verpa bohemica, *Ann. Myc.*, **12**: 241–250, *pl. 12.*

KONOKOTINA, A. G., 1913, O novikh drozhzhevikh gribkakh: Nadsonia (Guillermondia) elongata i Debaryomyces tryocola, *Izvest. Glavn. Botan. Sad*, **13**: 32–46, *pl.* 2.

KOSAROFF, P., 1907, Beitrag zur Biologie von Pyronema confluens, *Arb. Biol. Reichsanst. Land-u. Forstw.*, **5**: 126–138.

KRÜGER, F., 1908, Untersuchungen über die Fusskrankheit des Getreides, *Arb. biol. Reichsanst. Land-u. Forstw.*, **6**: 321–351.

———, 1910, Beitrag zur Kenntnis der Kernverhältnisse von Albugo candida und Peronospora Ficariae, *Centralbl. Bact. II Abt.*, **27**: 186–205, *pl. 1–2.*

KÜHNER, R., 1926, Contribution à l'étude des Hyménomycétes et spécialement des Agaricacés, *Le Botaniste*, **17**: 1–215, *pl. 1–4.*

———, 1927, Étude cytologique de l'hyménium de Mycena galericulata Scop., *Le Botaniste*, **18**: 169–176, *pl. 5.*

———, 1927*a*, Le développement du Boletinus cavipes (Opat.) Kalchb., *Le Botaniste*, **18**: 177–181, *pl. 6–7.*

KUNKEL, L. O., 1914, Nuclear behavior in the promycelia of Caeoma nitens Burrill and Puccinia Peckiana Howe, *Amer. Jour. Botany*, **1**: 37–47, *pl. 3.*

———, 1915, A contribution to the life history of Spongospora subterranea, *Jour. Agr. Res.*, **4**: 265–278, *pl. 29, 40–43.*

———, 1918, Tissue invasion by Plasmodiophora Brassicae, *Jour. Agr. Res.*, **14**: 543–572, *pl. 61–80.*

———, 1920, Further data on the orange-rusts of Rubus, *Jour. Agr. Res.*, **19**: 501–512, *pl. D., 92–94.*

KURSANOV, L. I., 1910, Zur Sexualität der Rostpilze, *Zeitschr. f. Botanik*, **2**: 81–93, *pl. 1.*

———, 1914, Über die Peridienentwicklung im Aecidium, *Ber. Deutsch. Botan. Ges.*, **32**: 317–327, *pl. 6.*

———, 1915, Morfologicheskiia i tsitologicheskiia izsledovaniia v gruppe Uredineae, [Moscow], 229 p., *6 pl.*

———, 1916, K istorii razvitiia rzhavchinnikov s povtorym obrazovaniem etsidiev, *Zhurn. Russk. Botan. Obshchestva*, **1**: 1–17, *pl. 1–2.*

———, 1922, Recherches morphologiques et cytologiques sur les urédinées, *Bull. Soc. Nat. Moscou, nouv. sér.* [1917], **31**: 1–129.

KUSANO, S., 1907, On the cytology of Synchtrium, *Centralbl. Bakt. II Abt.*, **19**: 538–543, *1 pl.*

———, 1908, On the nucleus of Synchytrium Puerariae, *Bot. Mag. Tokyo*, **21**: 118–121.

———, 1908, Studies on a disease of Pueraria caused by Synchytrium Puerariae, *Bot. Mag. Tokyo*, **22**: 1–3, *pl. 1.*

———, 1912, On the life-history and cytology of a new Olpidium with special reference to the copulation of motile isogametes, *Jour. Coll. Agr. Tokyo*, **4**: 141–199, *pl. 15–17.*

KUYPER, H. P., 1905, Die Perithecienentwicklung von Monascus purpureus Went und Monascus Barkeri Dangeard sowie die systematische Stellung dieser Pilze, *Ann. Myc.*, **3**: 32–81, *pl. 2.*

KYLIN, H., 1917, Generationswechsel und Kernphasenwechsel, *Die Naturwiss.*, **5**: 84–88.

LAFAR, F., 1905, Handbuch der technischen Mykologie [Jena].

LAFFERTY, H. A., and G. H. PETHYBRIDGE, 1922, On a Phytophthora, parasitic on apples which has both amphigynous and paragynous antheridia; and on allied species which show the same phenomenon, *Sci. Proc. R. Dublin Soc.*, **17**: 29–43, *pl. 1–2.*

LAGARDE, J., 1906, Contribution à l'étude des Discomycètes charnus, *Ann. Myc.*, **4**: 125–256.

LAGERHEIM, G. DE., 1892, Dipodascus albidus eine neue, geschlechtliche Hemiascee, *Jahrb. Wiss. Botanik*, **24**: 549–565, *pl. 24–26.*

———, 1893, Rhodochytrium nov. gen., eine Übergangsform von den Protococcaceen zu den Chytridiaceen, *Botan. Zeitung*, **51**: 43–52, *pl. 2.*

———, 1898, Mykologische Studien I, *Bih. Svensk. Vet. Akad. Handl.*, **24**: *Afd. III, no. 4,* 1–22.

———, 1899, Mykologische Studien II, *Bih. Svenska Vet. Akad Handl*, **25**: *Afd. III, no. 8:* 1–42, *pl. 1, 2.*

———, 1903, Zur Kenntnis der Bulgaria globosa, *Botan. Notiser*, **1903**: 249–267.

LAGERHEIM, G. DE, and N. PATOUILLARD, 1892, Sirobasidium, nouveau genre d' Hyménomycètes Hétérobasidiés, *Jour. de Botanique* [Morot], **6**: 465–469.

LAIBACH, F., 1920, Untersuchungen über einige Septoriaarten und ihre Fähigkeit zur Bildung höherer Fruchtformen I, II, *Zeitschr. f. Pflanzenkrankh.*, **30**: 201–223.

———, 1926, Zur Zytologie von Monoblepharis, *Ber. Deutsch. Botan. Ges.*, **44**: (59)–(64), *3 fig.*

LAKON, G., 1915, Zur Systematik der Entomophthoreengattung Tarichium, *Zeitschr. Pflanzenkrankh*, **25**: 257–272.

———, 1926, Über die systematische Stellung der Pilzgattung Basidiobolus Eidam, *Jahrb. Wiss. Botanik*, **65**: 388–400.

LANG, W., 1917, Über die Beeinflussung der Wirtspflanze durch Tilletia Tritici, *Zeitschr. f. Pflanzenkrankh*, **27**: 80–99.

LECHMÈRE, A. E., 1913, Description de quelques moisissures nouvelles provenant de la Côte d'Ivoire, *Bull. Soc. Myc. France*, **29**: 42–54; 303–331, *pl. 20–21*.

LÉGER, M., 1895, Structure et développement de la zygospore du Sporodinia grandis, *Rev. Gén. Botanique*, **7**: 481–496, *pl. 18–21*.

LEHFELD, W., 1923, Über die Entstehung des Paarkernmyzels bei heterothallischen Basidiomyceten, *Hedwigia*, **64**: 30–51, *pl. 1*.

LEHMAN, S. G., 1918, Conidial formation in Sphaeronema fimbriatum, *Mycologia*, **10**: 155–163, *pl. 7*.

LEININGER, H., 1911, Zur Morphologie und Physiologie der Fortpflanzung von Pestalozzia palmarum, *Centralbl. Bact. II Abt.*, **29**: 3–35.

LEITGEB, M. H., 1882, Completoria complens Lohde, ein in Farnprothallien schmarotzender Pilz, *Sitzungsber. Akad. Wiss. Wien. Math. Nat. Kl. I Abt.*, **84**: 288–324, *1 pl.*

LENDNER, A., 1908, Les Mucorinées de la Suisse, *Matér. flore crypt. suisse*, **3**[1]: 1–177.

———, 1920, A propos de l'hétérothallisme des coprins, *Bull. Soc. Bot. Genève*, 2 *sér.*, **12**: 336–352.

LEONIAN, L. H., 1925, Physiological studies on the genus Phytophthora, *Amer. Jour. Botany*, **12**: 444–498, *pl. 45–57*.

LEVINE, M., 1913, Studies in the cytology of the Hymenomycetes, especially the Boleti, *Bull. Torrey Botan. Club*, **40**: 137–181, *pl. 4–8*.

———, 1914, The origin and development of the lamellae in Coprinus micaceus, *Amer. Jour. Botany*, **1**: 343–356, *pl. 39–40*.

———, 1922, The origin and development of lamellae in Agaricus campestris and certain species of Coprinus, *Amer. Jour. Botany*, **9**: 509–533, *pl. 28–35*.

LEVISOHN, I., 1927, Beitrag zur Entwicklungsgeschichte und Biologie von Basidiobolus ranarum Eidam, *Jahrb. Wiss. Botanik*, **66**: 513–554.

LEWIS, C. E., 1906, The basidium of Amanita bisporigera, *Botan. Gaz.*, **41**: 348–352.

———, 1910, Occurrence of Monascus Barkeri in bottled pickles, *Mycologia*, **2**: 174.

LEWIS, I. M., 1911, The development of the spores in Pleurage zygospora, *Botan. Gaz.*, **51**: 369–373, *pl. 19*.

LEWTON-BRAIN, L., 1901, Cordyceps ophioglossoides, *Ann. Botany*, **15**: 521–531, *pl. 28*.

LIKHITÉ, V., 1926, Recherches sur le développement et la biologie de quelques Ascomycètes, *Rev. Gén. Botanique*, **38**: 5–30; 95–106; 146–163; 191–201; 239–251, *pl. 1–8*.

LINDAU, G., 1888, Über die Anlage und Entwickelung einiger Flechtenapothecien, *Flora*, **71**: 451–489, *1 pl.*

———, 1897, Phacidiineae, [Engler & Prantl] *Die Nat. Pfl. fam. I*, **1**: 243–265.

———, 1897*a*, Pyrenomycetineae, [Engler & Prantl] *Die Nat. Pfl. fam. I*, **1**: 321–491.

———, 1899, Beiträge zur Kenntnis der Gattung Gyrophora, [*Schwendener Festschrift*], 19–37, *2 pl.*

———, 1900, Fungi imperfecti, [Engler & Prantl] *Die Nat. Pfl. fam. I*, **1****: 347–523.

———, 1907–1910, Fungi imperfecti, [Rabenhorst] *Krypt fl. Deutsch. I*, **8**: 852 p.; **ꝺ**: 983 p.

LINDAU, G., and E. RIEHM, 1921, Die pflanzlichen Parasiten, [Sorauer] *Handb. d. Pflanzenkrankh., ed.*, 4, **2**.

LINDFORS, T., 1920, Einige bemerkenswerte, aus Kulturerde isolierte Pilze, *Svensk Botan. Tidskr.*, **14**: 267–276.

———, 1924, Studien über den Entwicklungsverlauf bei einigen Rostpilzen aus zytologischen und anatomischen Gesichtspunkten, *Svensk Botan. Tidskr.*, **18**: 1–84, *pl. 1–5.*

LOEWENTHAL, W., 1903, Beiträge zur Kenntnis des Basidiobolus lacertae, *Arch. f. Protistenk.*, **2**: 364–420.

———, 1905, Weitere Untersuchungen an Chytridiaceen, *Arch. f. Protistenk.*, **5**: 221–239, *pl. 7–8.*

LOHWAG, H., 1924, Der Übergang von Clathrus zu Phallus, *Arch. f. Protistenk.*, **49**: 237–259.

———, 1924*a*, Entwicklungsgeschichte und systematische Stellung von Secotium agaricoides, *Österr. Botan. Zeitschr.*, **73**: 161–174.

———, 1926, Zur Homologisierung der Konidien von Ascoidea, Ein Beitrag zum Verständnis endogener Zellbildung, *Biologia Generalis*, **2**: 835–864.

LOTSY, J. P., 1907, Vorträge über botanische Stammesgeschichte, [Jena]. **1**: 1–828, *430 figs.*

LUDWIG, C. A., and C. C. REES, 1918, The structure of the uredinium in Pucciniastrum Agrimoniae, *Amer. Jour. Botany*, **5**: 55–60, *pl. 8.*

LÜDI, R., 1901, Beiträge zur Kenntnis der Chytridiaceen, *Hedwigia*, **40**: 1–44, *pl. 1–2.*

LUPO, P., 1922, Stroma and formation of perithecia in Hypoxylon, *Botan. Gaz.*, **73**: 486–495, *pl. 18.*

LUTMAN, B. F., 1910, Some contributions to the life history and cytology of the smuts, *Trans. Wisconsin Acad. Sci.*, **16**: 1191–1244, *pl. 88–95.*

———, 1913, Studies on club-root I, The relation of Plasmodiophora Brassicae to its host and structure and growth of its plasmodium, *Vermont Agr. Exp. Sta. Bull.*, 175.

LYMAN, G. R., 1907, Culture studies on the polymorphism of Hymenomycetes, *Proc. Boston Soc. Nat. Hist.*, **33**: 125–209.

MCALPINE, B., 1905, A new genus of Uredineae, Uromycladium, *Ann. Myc.*, **3**: 303–323, *pl. 6–9.*

MCCUBBIN, W. A., 1910, Development of the Helvellineae 1, Helvella elastica, *Botan. Gaz.*, **49**: 195–206, *pl. 14–16.*

MCDOUGALL, W. B., 1919, Development of Stropharia epimyces, *Botan. Gaz.*, **67**: 258–263.

MAGNUS, W., 1906, Über die Formbildung der Hutpilze, *Arch. f. Biontologie*, **1**: 85–161.

MAIRE, R., 1899, Sur les phénomènes cytologiques précédant et accompagnant la formation de la teleutospore chez le Puccinia Liliacearum, *Comptes Rendus Acad. Sci.* [Paris], **129**: 839–841.

———, 1900, L'évolution nucléaire chez les Endophyllum, *Jour. de Botanique* [*Morot*], **14**: 80–92; 93–97; 369–382, *pl. 4.*

———, 1902, Recherches cytologiques et taxonomiques sur ler Basidiomycètes, *Thèse* [Paris], 209 p.

———, 1905, Recherches cytologiques sur quelques Ascomycètes, *Ann. Myc.*, **3**: 123–154, *pl. 3–5.*

———, 1906, Remarques sur quelques Erysiphacées, *Bull. Séances Soc. Sci. Nancy 3 sér.*, **6**: 31–37, *pl. 2.*

———, 1908, Les suçoirs des Meliola et des Asterina, *Ann. Myc.*, **6**: 124–128.

———, 1911, La biologie des Urédinales, *Progr. Rei. Botan.*, **4**: 109–162.

———, 1911*a*, Remarques sur quelques Hypocréacées, *Ann. Myc.*, **9**: 315–325, *pl. 16.*

MAIRE, R., and A. TISON, 1909, La cytologie des Plasmodiophoracées et la classe des Phytomyxineae, *Ann. Myc.*, **7**: 226–253.

MAIRE, R., AND A. TISON, 1911, Nouvelles recherches sur les Plasmodiophoracées, *Ann. Myc.*, **9**: 226–246, *pl. 10–14*.

MALINOWSKI, E., 1913, Sur la division des noyaux de 'Cyathus, *Comptes rendus Séanc. Soc. Sci. Varsovie*, **6**: 590–597.

MANGENOT, G., 1922, A propos de quelques formes peu connues d'Endomycétacées, *Bull. Soc. Myc. France*, **38**: 42–54, *pl. 1, 2*.

MANGIN, L., 1910, Qu'est ce que l'Aspergillus glaucus? *Ann. Sci. Nat. Bot., sér. 9.*, **10**: 303–371.

MARCHAND, H., 1913, La conjugaison des spores chez les levures, *Rev. Gén. Botanique*, **25**: 207–222.

MARTIN, E. M., 1924, Cytological studies of Taphrina Coryli, *Trans. Wisconsin Acad. Sci.*, **21**: 345–356.

———, 1925, Cultural and morphological studies of some species of Taphrina, *Phytopathology*, **15**: 67–76.

MARTIN, G. W., 1925, Morphology of Conidiobolus villosus, *Botan. Gaz.*, **80**: 311–318, *pl. 16*.

———, 1927, Basidia and spores of the Nidulariaceae, *Mycologia*, **19**: 239–247, *pl. 22–23*.

MASSEE, G., 1900, On the origin of the Basidiomycetes, *Jour. Linn. Soc. Botany*, **34**: 438–448, *pl. 15–16*.

———, 1909, The structure and affinities of British Tuberaceae, *Ann. Botany*, **23**: 243–263, *pl. 17*.

MASSEE, I., 1914, Observations on the life history of Ustilago Vaillantii Tul., *Jour. Econom. Biol.*, **9**: 7–14, *pl. 1*.

MATRUCHOT, L., 1897, Recherches biologiques sur les champignons, *Rev. Gén. Botanique*, **9**: 81–102, *pl. 1*.

MATRUCHOT, L., and C. DASSONVILLE, 1899, Sur le Ctenomyces serratus Eidam comparé aux champignons des teignes, *Bull. Soc. Myc. France*, **15**: 305–310.

———, 1899, Sur le champignon de l'Herpès [Trichophyton] et les formes voisines, et sur la classification des Ascomycètes, *Bull. Soc. Myc. France*, **15**: 240–253.

———, 1900, Sur une forme de reproduction d'ordre élevé chez les Trichophyton, *Bull. Soc. Myc. France*, **16**: 201–208.

———, 1901, Eidamella spinosa, dermatophyte produisant des périthèces, *Bull. Soc. Myc. France*, **17**: 123–132, *pl. 5*.

MATTIROLO, O., 1903, I funghi ipogei italiani raccolti da O. Beccari, L. Caldesi, A. Carestia, V. Cesati, P. A. Saccardo, *Mem. R. Accad. Sci. Torino, ser.* 2, **53**: 331–366, *1 pl.*

———, 1912, Jaczewskia, illustrazione di un nuovo genere di Histerangiaceae, *Mem. R. Accad. Sci. Torino, ser.* 2, **63**: 213–218, *1 pl.*

MAURIZIO, A., 1894, Zur Entwicklungsgeschichte und Systematik der Saprolegnieen, *Flora*, **79**: 109–158, *pl. 3–5*.

MAYUS, O., 1903, Die Peridienzellen der Uredineen in ihrer Abhängigkeit von Standortsverhältnissen, *Centralbl. Bact. II Abt.*, **10**: 644–655; 700–721.

MELHUS, J. E., 1911, Experiments on spore germination and infection in certain species of Oomycetes, *Univ. Wisconsin Agr. Exp. Stat. Res. Bull.*, **15**: 25–84.

———, 1914, A species of Rhizophidium parasitic on the oospores of various Peronosporeae, *Phytopathology*, **4**: 55–62, *pl. 4*.

MEYER, A., 1902, Die Plasmaverbindungen und die Fusionen der Pilze der Florideenreihe, *Bot. Zeitung*, **60**: 139–178, *pl. 6*.

MEYER, B., 1888, Untersuchungen über die Entwicklung einiger parasitischer Pilze, *Landw. Jahrb.*, **17**: 915–945.

MILBURN, T., 1904, Über Änderungen der Farben bei Pilzen und Bakterien, *Centralbl. Bact. II Abt.*, **13**: 129–138; 257–276, *2 pl.*

MINDEN, M. VON, 1911–15, Chytridiineae, Ancylistineae, Monoblepharidineae, Saprolegniineae, *Krypt. fl. Mark Brandenburg*, **5**: 209–630.

———, 1916, Beiträge zur Biologie und Systematik einheimischer submerser Phycomyceten, [Falck] *Mykol. Unters. u. Ber.*, **1**: 146–255, *pl. 1–8*.

MIYAKE, K., 1901, The fertilization of Pythium debaryanum, *Ann. Botany*, **15**: 653–667, *pl. 36*.

MÖLLER, A., 1888, Über die sogenannten Spermatien der Ascomyceten, *Botan. Zeitung*, **46**: 421–425.

———, 1887, Über die Cultur flechtenbildender Ascomyceten ohne Algen, *Inaug.-Diss. Münster*, 52 p., *K. Akad. Münster i. W.*

———, 1893, Über die eine Thelephoree, welche die Hymenolichenen: Cora, Dictyonema und Laudatea bildet, *Flora*, **77**: 254–278.

———, 1893, Die Pilzgärten einiger südamerikanischer Ameisen, *Botan. Mitt. a. d. Tropen* [Schimper], **6**: 1–127, *7 pl.*

———, 1895, Brasilische Pilzblumen, *Botan. Mitt. a. d. Tropen* [Schimper], **7**: 1–152, *pl. 1–8*.

———, 1895, Protobasidiomyceten, *Botan. Mitt. a. d. Tropen* [Schimper], **8**: 1–179, *pl. 1–6*.

———, 1901, Phycomyceten und Ascomyceten. Untersuchungen aus Brasilien, *Botan. Mitt. a. d. Tropen* [Schimper], **9**: 1–319, *11 pl.*

MOLLIARD, M., 1909, Le cycle de développement du Crucibulum vulgare Tul. et de quelques champignons supérieurs obtenu en cultures pures, *Bull. Soc. Botanique France*, **56**: 91–96.

MOREAU, F., 1913, Étude histologique de la bulbillose des lames chez un agaric, *Bull. Soc. Myc. France*, **29**: 341–344.

———, 1913, Recherches sur la réproduction des Mucorinées et de quelques autres thallophytes, *Le Botaniste*, **13**: 1–136.

———, 1914, Sur le développement du périthèce chez une Hypocreale, le Peckiella lateritia (Fries) Maire, *Bull. Soc. Botanique, France*, **61**: 160–164, *pl. 2*.

MOREAU, MME. F., 1914, Les phénomènes de la sexualité chez les urédinées, *Le Botaniste*, **13**: 145–284.

MOREAU, F. and MME. F., 1915, L'évolution nucléaire et les phénomènes de la sexualité chez les lichens du genre Peltigera, *Comptes Rendus Acad. Sci.* [Paris], **160**: 526–528.

———, 1916, Les phénomènes de la sexualité chez les lichens du genre Solorina, *Comptes Rendus Acad. Sci.* [Paris], **162**: 793–795.

———, 1918, Étude cytologiques de l'apothécie des Peltigéracées, *Comptes Rendus Acad. Sci.* [Paris], **166**: 178–179.

———, 1918, L'écidiospore de l'Endophyllum Euphorbiae-silvaticae (DC.) Winter, est-elle le siège d'une karyogamie?, *Bull. Soc. Myc. France*, **33**: 97–99.

———, 1919, Les urédinées du groupe Endophyllum, *Bull. Soc. Botanique France*, **66**: 14–44.

———, 1922, Le mycélium à boucle chez les Ascomycètes, *Comptes Rendus Acad. Sci.* [Paris], **174**: 1072–1074.

MORGENTHALER, O., 1910, Über die Bedingungen der Teleutosporenbildung bei den Uredineen, *Centralbl. Bact. II*, **27**: 73–92.

MOSS, E. H., 1923, Developmental studies in the genus Collybia, *Trans. Roy. Canadian. Inst.*, **14**: 321–335, *pl. 24–26*.

———, 1926, The uredo stage of the Pucciniastreae, *Ann. Botany*, **40**: 813–847, *pl. 34*.

MOUNCE, I., 1921, Homothallism and the production of fruit bodies by monosporous mycelia in the genus Coprinus, *Trans. British Myc. Soc.*, **7**: 198–217, *pl. 6–7*.

———, 1922, Homothallism and heterothallism in the genus Coprinus, *Trans. British Myc. Soc.*, **7**: 256–269.

MÜCKE, M., 1908, Zur Kenntnis der Eientwicklung und Befruchtung von Achlya polyandra de Bary, *Ber. Deutsch. Botan. Ges.*, **26a**: 367–378, *pl. 6.*

MÜLLER, K., 1913, Zur Biologie der Schwarzfleckenkrankheit der Ahornbäume hervorgerufen durch den Pilz Rhytisma acerinum, *Centralbl. Bact. II Abt.*, **36**: 67–98, *pl. 1–4.*

MUNK, M., 1912, Über die Bedingungen der Koremienbildung bei Penicillium, *Myc. Centralbl.*, **1**: 387–403.

MURPHY, P. A., 1918, The morphology and cytology of the sexual organs of Phytophthora erythroseptica, *Ann. Botany*, **32**: 115–153.

———, 1922, The bionomics of the conidia of Phytophthora infestans (Mont.) de Bary, *Sci. Proc. R. Dublin Soc. N. S.*, **16**: 442–466.

NADSON, G. A., 1911, Polovoi protsess u drozhzhei i bakterii, *Russkii Vrach*, **31**: 1–35. [Rev. TRANZSCHEL, W., Der sexuelle Prozess bei den Hefepilzen und Bacterien, *Myk. Centralbl.* [1912], **1**: 148–150, *f. 11.*]

NADSON, G. A. and A. G. KONOKOTINA, 1911, O novom rode drozhzhevykh gribkov Guillermondia, s heterogamnoi kopulatsiei. *Izvestiia Imp. St. Petersb. Botan. Sad*, **11**: 117–143, *45 fig.*, [Rev. *Centralbl. Bact. II Abt.*, **34**: 241–242].

NAVASHIN, S., 1899, Beobachtungen über den feineren Bau und Umwandlungen von Plasmodiophora Brassicae Woron. im Laufe ihres intracellularen Lebens, *Flora*, **86**: 404–427, *pl. 30.*

NEGER, F. W., 1901, Beiträge zur Biologie der Erysipheen I, *Flora*, **88**: 333–370, *pl. 15–16.*

———, 1902, Beiträge zur Biologie der Erysipheen II, *Flora*, **90**: 221–272.

———, 1914, Über Urocystis-ähnliche Nebenfruchtformen von Hypocreaceen, *Myc. Centralbl.*, **4**: 273–278.

———, 1918, Experimentelle Untersuchungen über Russtaupilze, *Flora*, **110**: 67–139.

NĚMEC, B., 1911, Zur Kenntnis der niederen Pilze I, *Česka Akad. Cisaře Františka Josefa pro Vědy Slovesnost a Uměni v Praze, Bull. internat.*, **16**: 67–85; 118–127; 136–144.

———, 1912, *Ibid.*, **17**: 16–25.

———, 1913, *Ibid.*, **18**: 18–31; 32–43.

———, 1922, Sexuality in Olpidium Brassicae, *Zolastni Otisk ze Sborniku Kiubu Praze*, **1920**: 1–3.

NEUHOFF, W., 1924, Zytologie und systematische Stellung der Auriculariaceen und Tremellaceen, *Botan. Arch.*, **8**: 250–297.

NEWTON, D. E., 1926, The bisexuality of individual strains of Coprinus Rostrupianus, *Ann. Botany*, **40**: 105–128, *pl. 6.*

NICHOLS, M. A., 1896, The morphology and development of certain pyrenomycetous fungi, Botan. *Gaz.*, **22**: 301–328, *pl. 14–16.*

NICHOLS, S. P., 1905, The nature and origin of the binucleated cells in some Basidiomycetes, *Trans. Wisconsin Acad. Sci.* [1904], **15**: 30–61.

NIENBURG, W., 1908, Beiträge zur Entwicklungsgeschichte einiger Flechtenapothecien, *Flora*, **98**: 1–40, *pl. 1–7.*

———, 1913, Symbiose, [Flechten], *in Handwörterbuch d. Naturw.*, **9**: 929–941.

———, 1914, Zur Entwicklungsgeschichte von Polystigma rubrum, *Zeitschr. f. Botanik*, **6**: 369–400.

NOWAKOWSKI, L., 1876, Beitrag zur Kenntnis der Chytridiaceen, *Beitr. Biol. Pfl.*, [Cohn], **2**: 73–100, *pl. 4–6.*

NYPELS, 1897, Le germination de quelques écidiospores, *Ann. Soc. Belge de Microsc.*, **21**: 103–111.

OBEL, P., 1910, Researches on the conditions of the forming of oogonia in Achlya, *Ann. Myc.*, **8**: 421–443.

OLIVE, E. W., 1905, The morphology of Monascus purpureus, *Botan. Gaz.*, **39**: 56–60.
———, 1906, Cytological studies on the Entomophthoreae: 1, Morphology and development of Empusa, *Botan. Gaz.*, **41**: 192–208; 2, Nuclear and cell division of Empusa., *Ibid.* **41**: 229–261, *pl. 14–16.*
———, 1907, Cell and nuclear division in Basidiobolus, *Ann. Myc.*, **5**: 404–418, *pl. 10.*
———, 1908, Sexual cell fusions and vegetative nuclear divisions in the rusts, *Ann. Botany*, **22**: 331–360, *pl. 22.*
———, 1911, The nuclear conditions in certain short cycled rusts, *Sci. N. S.*, **33**: 194.
———, 1913, Intermingling of perennial sporophytic and gametophytic generations in Puccinia Podophylli, P. obtegens and Uromyces Glycyrrhizae, *Ann. Myc.*, **11**: 297–311, *pl. 15.*
———, 1918, The cytological structure of Botryorhiza, *Mem. Brooklyn Botan. Gard.*, **1**: 337–341.
OLTMANNS, F., 1887, Über die Entwickelung der Perithecien in der Gattung Chaetomium, *Botan. Zeitung.*, **45**: 193–200; 209–218; 225–233; 249–254; 265–271; *pl. 3.*
ORTON, C. R., 1924, Studies in the morphology of the Ascomycetes I, The stroma and the compound fructification of the Dothideaceae and other groups, *Mycologia*, **16**: 49–95, *pl. 7–9.*
———, 1927, A working hypothesis on the origin of rusts with special reference to the phenomenon of heteroecism, *Botan. Gaz.*, **84**: 113–138.
OSBORN, T. G. B., 1911, Spongospora subterranea, *Ann. Botany*, **25**: 327–341, *pl. 27.*
OVERHOLTS, L. O., 1915, Comparative studies in the Polyporaceae, *Ann. Missouri Botan. Gard.*, **2**: 667–730, *pl. 23–25.*
OVERTON, J. B., 1906, The morphology of the ascocarp and spore formation in the many-spored asci of Thecotheus Pelletieri, *Botan. Gaz.*, **42**: 450–492, *pl. 29, 30.*
PALLA, E., 1899, Über die Gattung Phyllactinia, *Ber. Deutsch. Botan. Ges.*, **17**: 64–72, *pl. 5.*
PARAVICINI, E., 1917, Untersuchungen über das Verhalten der Zellkerne bei der Fortpflanzung der Brandpilze, *Ann. Myc.*, **15**: 57–96, *pl. 1–6.*
PARKER, G. H., 1887, On the morphology of Ravenelia glandulaeformis, *Proc. Amer. Acad. Sci.*, **22**: 205–219, *pl. 1–2.*
PATOUILLARD, N., 1892, Septobasidium, nouveau genre d'Hyménomycètes Hétérobasidiés, *Jour. de Botanique* [Morot], **8**: 61–64.
———, 1900, Essai taxonomique sur les familles et les genres des Hyménomycètes, *Thèse pharm.* [Paris], 184 p.
———, 1913, Sur un Septobasidium conidifère, *Comptes Rendus Acad. Sci.* [Paris], **156**: 1699–1701.
PAVILLARD, J., 1910, État actuel de la protistologie végétale, *Progr. Rei Botan.*, **3**: 474–544.
———, 1912, À propos de la phylogénie des Plasmodiophoracées, *Ann. Myc.*, **10**: 218–219.
PÉNAU, H., 1912, Contribution à la cytologie de quelques microorganismes, *Rev. Gén. Botanique*, **24**: 13–95.
PENZIG, O., 1899, Über javanische Phalloideen, *Ann. Jard. Bot. Buitenzorg*, **16**: 133–173, *pl. 16–25.*
PETCH, T., 1907, Hydnocystis Thwaitesii, *Ann. Myc.*, **5**: 473–475.
———, 1908, The Phalloideae of Ceylon, *Ann. R. Botan. Gard. Peradeniya*, **4**: 139–184.
———, 1911, Note on the biology of the genus Septobasidium, *Ann. Botany*, **25**: 843.
———, 1924, Studies in entomogenous fungi V, Myriangium, *Trans. British Myc. Soc.*, **10**: 45–80, *pl. 2–3.*
———, 1926, Matula, *Trans. British Myc. Soc.*, **11**: 67–81, *pl. 2–3.*
———, 1926, Mutinus bambusinus (Zoll.), Ed. Fischer, *Trans. British Myc. Soc.*, **10**: 272–282, *pl. 14–16.*

PETERSEN, H. E., 1905, Contributions à la connaissance des phycomycètes marins (Chytridineae Fischer), *Oversigt over det K. Danske Vidensselsk. Forh.*, **1905**: 439–488.

———, 1910, An account of Danish freshwater-Phycomycetes, *Ann. Myc.*, **8**: 494–560.

PETHYBRIDGE, G. H., 1913, On the rotting of potato tubers by a new species of Phytophthora having a sexual reproduction hitherto undescribed, *Sci. Proc. R. Dublin Soc. N. S.*, **13**: 529–565.

———, 1914, Further observations on Phytophthora erythroseptica Pethybr. and on the disease produced by it in the potato plant, *Sci. Proc. R. Dublin Soc. N. S.*, **14**: 179–198.

PETHYBRIDGE, G. H. and P. A. MURPHY, 1913, On pure cultures of Phytophthora infestans De Bary and the development of oospores, *Sci. Proc. R. Dublin Soc. N. S.*, **13**: 566–588.

PETRAK, F., 1921, Mykologische Notizen III, *Ann. Myc.*, **19**: 176–223.

———, 1923, Mykologische Notizen V, *Ann. Myc.*, **21**: 1–69.

PETRI, L., 1902, La formazione delle spore nell' Hydnangium carneum, *N. Giorn. Botan. Ital.*, **9**: 499–514, *pl. 14*.

———, 1904, Sul valore diagnostico del capillizio nel genere Tylostoma, *Ann. Myc.*, **2**: 412–438, *pl. 6*.

PILLAY, T. P., 1923, Zur Entwicklungsgeschichte von Sphaerobolus stellatus, *Jahrb. Phil. Fak. II Bern.*, **3**: 197–219, *pl. 1*.

POIRAULT, G., 1913, Sur quelques uredinées nouvelles, *Bull. Ass. Nat. Nice Alpes Maritimes*, **120**: 105–108.

———, 1915, Sur quelques champignons rares ou nouveaux observés dans les Alpes Maritimes, *Bull. Ass. Nat. Nice Alpes Maritimes*, **2³**: 7–19.

POIRAULT, G., and M. RACIBORSKI, 1895, Sur la noyaux des urédinées, *Journ. de Botanique* [Morot], **9**: 318–332; 381–388, *pl. 6*.

POLE-EVANS, J. B., and A. M. BOTTOMLEY, 1918, On the genera Diplocystis and Broomeia, *Trans. R. Soc. South Africa*, **7**: 189–192, *pl. 19-22*.

POPTA, C. M. L., 1899, Beitrag zur Kenntnis der Hemiasci, *Flora*, **86**: 1–46, *pl. 1–2*.

POTEBNIA, A. A., 1908, K istorii razvitiia nekotorykh askomitsetov 1. Mycosphaerella, 2. Gnomonia, Glomerella i Pseudopeziza, *Trudy Obshchestva Ispytatelei Prirody, Imp. Kharkov. Univ.*, **42**: 1–151, *63 f.*

———, 1910, Beiträge sur Micromycetenflora Mittel-Russlands, *Ann. Myc.*, **8**: 42–93.

———, 1912, Ein neuer Krebserreger des Apfelbaumes Phacidiella discolor (Mont. et Sacc.) A. Pot., seine Morphologie und Entwicklungsgeschichte, *Zeitschr. f. Pflanzenkrankh.*, **22**: 129–148, *pl. 1–3*.

PRILLIEUX, M., 1904, Sur la déhiscence des périthèces du Rosellinia necatrix (R. Hart.), Berlese, *Bull. Soc. Myc. France*, **20**: 34–38, *pl. 3–4*.

PRINGSHEIM, N., 1858, Über das Austreten der Sporen von Sphaeria Scirpi aus ihren Schläuchen, *Jahrb. Wiss. Botanik*, **1**: 189–192.

PROWAZEK, S., 1902, Zur Kernteilung der Plasmodiophora Brassicæ, *Österr. Botan. Zeitschr.*, **52**: 213–217.

———, 1905, Über den Erreger der Kohlhernie Plasmodiophora Brassicae Woronin und die Einschlüsse in den Carcinomzellen, *Arbeit. Kais. Gesundheitsamt*, **22**: 396–410. *1 pl.*

RABINOWITSCH, L., 1894, Beiträge zur Entwicklungsgeschichte oder Fruchtkörper einiger Gastromyceten, *Flora*, **79**: 385–418, *pl. 10–11*.

RACIBORSKI, M., 1896, Über den Einfluss der äussern Bedingungen auf die Wachstumsweise des Basidiobolus ranarum, *Flora*, **82**: 107–132.

———, 1900, Parasitische Algen und Pilze Javas II [Batavia], 46 p.

RACIBORSKI, M., 1909, Parasitische und epiphytische Pilze Javas, *Bull. Acad. Int. Sci. Cracovie*, **1909**: 348–394.

RAMLOW, G., 1906, Zur Entwicklungsgeschichte von Thelebolus stercoreus Tode, *Botan. Zeitung*, **64**: 85–97, *pl. 4.*

———, 1915, Beiträge zur Entwicklungsgeschichte der Ascoboleen, *Myc. Centralbl.*, **5**: 177–198, *pl. 1–2.*

RANT, A., 1912, Über die Djamoer-oepas-Krankheit und über das Corticium javanicum Zimm., *Bull. Jard. Botanique Buitenzorg*, 2. *sér.*, **4**: 1–50. *9 pl.*

RAUNKIAER, C., 1918, En ny Tulasnella-Art samt Bemaerkninger om Tulasnella's systematiske Stilling, *Botan. Tidsskr.*, **36**: 204–212, *f. 1.*

RAVAZ, L., and G. VERGE, 1913, La germination des spores d'hiver de Plasmopara victiola, *Comptes Rendus Acad. Sci.* [Paris], **156**: 800–802.

RAWITSCHER, F., 1912, Beiträge zur Kenntnis der Ustilagineen, *Zeitschr. f. Botanik*, **4**: 678–700, *pl. 8.*

———, 1914, Zur Sexualität der Brandpilze, *Ber. Deutsch. Botan. Ges.*, **32**: 310–314, *4 fig.*

———, 1922, Beiträge zur Kenntnis der Ustilagineen, *Zeitschr. f. Botanik*, **14**: 273–296, *pl. 1–2.*

REA, C., 1922, British Basidiomycetae, a handbook to the larger British fungi, Cambridge, xi + 799 p.

REESS, M., and C. FISCH, 1887, Untersuchungen über Bau und Lebensgeschichte der Hirschtrüffel, Elaphomyces, *Bibliotheca Botan.*, **7**: 1–26. *1 pl.*

REHSTEINER, H., 1892, Beiträge zur Entwicklungsgeschichte der Fruchtkörper einiger Gastromyceten, *Botan. Zeitung*, **50**: 761–771; 777–792; 801–814; 823–839; 843–863; 865–878, *pl. 10–11.*

RICK, J., 1910, Die Gattung Geaster und ihre Arten, *Beih. Botan. Centralbl. II Abt.*, **27**: 375–383.

RIDDLE, L. W., 1907, On the cytology of the Entomophthoraceae, *Proc. Amer. Acad. Arts Sci.*, **42**: 177–198, *pl. 1–3.*

ROSE, L., 1910, Beiträge zur Kenntnis der Organismen im Eichenschleimfluss, *Inaug.-Diss. Berlin*, 50 p.

ROSEN, F., 1893, Beiträge zur Kenntnis der Pflanzenzellen, *Beitr. Biol. Pfl.* [Cohn], **6**: 237–266, *pl. 2–3.*

ROSENBAUM, J., 1917, Studies of the genus Phytophthora, *Jour. Agr. Res.*, **8**: 233–276, *pl.* 71–77.

ROSENBERG, O., 1903, Über die Befruchtung von Plasmopara alpina, *Bih. Svenska Vet. Akad. Handl.*, **28**: *Afd. 3, no. 10:* 1–20, *2 pl.*

ROSTOWZEW, S. I., 1903, Beiträge zur Kenntnis der Peronosporeen, *Flora*, **92**: 405–430, *pl. 11–13.*

ROTHERT, W., 1892, Die Entwicklung der Sporangien bei den Saprolegnieen, *Beitr. Biol. Pfl.* [Cohn], **5**: 291–349, *pl. 10.*

———, 1903, Die Sporentwicklung bei Aphanomyces, *Flora*, **92**: 293–301.

ROUGE, E., 1907, Le Lactarius sanguifluus Fr. et la lipase, *Centralbl. Bact. II Abt.*, **18**: 403–417.

ROUPPERT, C., 1909, Révision du genre Sphaerosoma, *Bull. Acad. Sci. Cracovie. Cl. Sci. Math. Nat.*, **1909**: 75–95.

RUHLAND, W., 1900, Untersuchungen zu einer Morphologie der stromabildenden Sphaeriales auf entwickelungsgeschichtlicher Grundlage, *Hedwigia*, **39**: 1–79, *pl. 1–3.*

———, 1901, Über die Ernährung und Entwicklung eines mycophthoren Pilzes Hypocrea fungicola, *Verh. Botan. Ver. Prov. Brandenburg*, **42**: 53–65, *pl. 3.*

———, 1901, Zur Kenntnis der intracellularen Karyogamie bei den Basidiomyceten, *Botan. Zeitung*, **59**: 187–206, *pl. 7.*

———, 1904, Studien über die Befruchtung der Albugo Lepigoni und einiger Peronosporeen, *Jahrb. Wiss. Botanik*, **39**: 135–166, *pl. 2–3.*

RUMBOLD, C., 1908, Beiträge zur Kenntnis der Biologie holzzerstörender Pilze, *Naturw. Zeitschr. f. Forst-u. Landw.*, **6**: 81–140.

———, 1911, Über die Einwirkung von Säure und Alkaligehaltes des Nährbodens auf das Wachstum der holzzersetzenden und holzverfarbenden Pilze; mit einer Erörterung über die systematischen Beziehungen zwischen Ceratostomella und Graphium, *Naturw. Zeitschr. f. Forst und Landw.*, **9**: 429–460, *22 f.*

RYAN, R. W., 1926, The development of the perithecia in the Microthyriaceae and a comparison with Meliola, *Mycologia*, **18**: 100–110, *pl. 12–15.*

RYTZ, W., 1907, Beiträge zur Kenntnis der Gattung Synchytrium, *Centralbl. Bakt. II Abt.*, **18**: 635–655; 799–825, *1 pl.*

———, 1917, Die cytologischen Verhältnisse bei Synchytrium Taraxaci deBy et Wor., *Beih. z. Botan. Zentralbl. Abt. II.*, **34**: 343–372, *pl. 2–4.*

SACHS, J., 1855, Morphologie des Crucibulum vulgare, *Bot. Zeitung*, **13**: 833–845; 849–861, *pl. 13–14.*

SADEBECK, R., 1884, Untersuchungen über die Pilzgattung Exoascus, *Jahrb. Hamburg. Wiss. Anst.*, **1**: 93–124, *pl. 1–4.*

———, 1893, Die parasitischen Exoasceen, *Jahrb. Hamburg. Wiss. Anst.* [1892], **10**^{2}: 1–110, *pl. 1–3.*

SÄTTLER, H., 1914, Untersuchungen und Erörterungen über die Ökologie und Phylogenie der Cladoniapodetien, *Hedwigia*, **54**: 226–263, *pl. 5–9.*

SALMON, E. S., 1900, A monograph of the Erysiphaceae, *Mem. Torrey Botan. Club*, **9**: 1–292, *pl. 1–9.*

———, 1903, The specialization of parasitism in the Erysiphaceae, I. *Beih. Botan. Centralbl., I. Abt.*, **14**: 261–315, *pl. 18.*

———, 1904, II, *New Phytol.* **3**: 109–121.

———, 1904*a*, Cultural experiments with biologic forms of the Erysiphaceae, *Phil. Trans. R. Soc. London, B.*, **197**: 107–122.

———, 1905, Cultural experiments with an Oidium on Euonymus japonicus, *Ann. Myc.*, **3**: 1–15, *pl. 1.*

———, 1906, On Oidiopsis taurica (Lév.) an endophytic member of the Erysiphaceae, *Ann. Botany*, **20**: 187–200, *pl. 13, 14.*

SANDS, M. C., 1907, Nuclear structure and spore formation in Microsphaera Alni, *Trans. Wisconsin Acad. Sci.*, **15**: 733–752, *pl. 46.*

SAPPIN-TROUFFY, P., 1896, Recherches mycologiques, *Le Botaniste*, **5**: 44–58.

———, 1896*a*, Recherches histologique sur la famille des Urédinees, *Le Botaniste*, **5**: 59–244.

SARTORIS, G. B., 1924, Studies in the life history and physiology of certain smuts. *Amer. Jour. Botany*, **11**: 617–647, *pl.* 39–41.

SATINA, S., 1921, Oplodotvorenie i istoriia razvitiia Cubonia brachyasca Sacc., *Zhurn. Russk. Botan. Obshchestva* [1918–19], **4**: 77–94, *2 pl.*

———, 1921*a*, K istorii razvitiia Phacidium repandum, *Zhurn. Russk. Botan. Obshchestwa.*, [1918–19], **4**: 95–102.

———, 1923, Beiträge zur Kenntnis der Ascomyceten, *Botan. Arch.*, **3**: 273–281.

SAWYER, W. H., 1917, The development of Cortinarius pholideus, *Amer. Jour. Botany*, **4**: 520–532, *pl. 28–29.*

———, 1917, Development of some species of Pholiota, *Botan. Gaz.*, **64**: 206–229, *pl. 16–20.*

SAX, H. [D. M.] JOLIVETTE, see JOLIVETTE-SAX, H. [D. M.].

SCHAFFNIT, E., 1912, Der Schneeschimmel und die übrigen durch Fusarium nivale Ces. hervorgerufenen Krankheitserscheinungen des Getreides, *Landw. Jahrb.*, **43**: 521–648, *5 pl.*

SCHAFFNIT, E., 1913, Zur Systematik von Fusarium nivale bzw. seiner höheren Fruchtform, *Myk. Centralbl.*, **2**: 253–258.

SCHELLENBERG, H. C., 1911, Die Brandpilze der Schweiz, *Beitr. Kryptog. Fl. Schweiz*, **3**^{2}: 1–325, *70 fig.*

———, 1912, Über die Schädigung der Weinrebe durch Valsa Vitis (Schweinitz) Fuckel, *Ber. Deutsch. Botan. Ges.*, **30**: 586–594, *pl.* 16.

———, 1917, Zur Kenntnis der Entwicklungsverhältnisse von Mycosphaerella Fragariae, *Vierteljahrs-schr. Naturf. Ges. Zürich*, **62**: 383–393, *pl. 8–9.*

SCHERFFEL, A., 1925, Endophytische Phycomycetenparasiten der Bacillariaceen und einige neue Monadinen, Ein Beitrag zur Phylogenie der Oomyceten, *Arch. f. Protistenk.*, **52**: 1–141, *pl. 1–5.*

SCHIKORRA, W., 1909, Über die Entwickelungsgeschichte von Monascus, *Zeitschr. f. Botanik*, **1**: 379–410, *pl. 2.*

SCHNEGG, H., 1915, Zur Entwicklungsgeschichte und Biologie der Pykniden, sowie der Schlingenmyceliен und Hyphenknäuel. Studien an einem häufigen Bräuerei-Saprophyten, *Centralbl. Bakt. II Abt.*, **43**: 326–364.

SCHRAMM, R., 1914, Über eine bemerkenswerte Degenerationsform von Aspergillus niger, *Myc. Centralbl.*, **5**: 20–27.

SCHRÖDER, B., 1898, Dangeardia, ein neues Chytridineengenus auf Pandorina morum Bory, *Ber. Deutsch. Botan. Ges.*, **16**: 314–321, *pl. 20.*

SCHROETER, J., 1875, Die Pflanzenparasiten aus der Gattung Synchytrium, *Beitr. Biol. Pfl.* [Cohn], **1**: 1–50, *pl. 1–3.*

———, 1876, Über die Entwicklung und die systematische Stellung von Tulostoma Pers., *Beitr. Biol. Pfl.* [Cohn], **2**: 65–72.

———, 1888, Die Pilze Schlesiens, **1**: 442–443. [Cohn, F., Kryptog. Fl. Schlesien, **3**^{1}: 442–443.]

SCHULTZ, E. S., 1927, Nuclear division and spore formation in the ascus of Peziza domiciliana, *Amer. Jour. Botany*, **14**: 307–322, *pl.* 35–39.

SCHUSSNIG, B., 1921, Ein Beitrag zur Kenntnis der Zytologie von Tuber aestivum Vitt., *Sitzungsber. Akad. Wiss. Wien. Math.-Nat. Kl. Abt.* 1, **130**: 127–146, *1 pl.*

SCHWARTZ, E. J., 1910, Parasitic root diseases of the Juncaceae, *Ann. Botany*, **24**: 511–522, *pl. 50.*

———, 1911, The life-history and cytology of Sorosphaera graminis, *Ann. Botany*, **25**: 791–797, *pl. 61.*

———, 1914, The Plasmodiophoraceae and their relationship to Mycetozoa and the Chytrideae, *Ann. Botany*, **28**: 227–240, *pl. 12.*

SCHWARZE, C. A., 1922, The method of cleavage in the sporangia of certain fungi, *Mycologia*, **14**: 143–172, *pl. 15–16.*

SCHWEIZER, G., 1923, Ein Beitrag zur Entwicklungsgeschichte und Biologie von Ascobolus nov. spec., *Zeitschr. f. Botanik*, **15**: 529–556.

SCHWEIZER, J., 1919, Die kleinen Arten bei Bremia lactucae Regel und ihre Abhängigkeit von Milieu-einflüssen, *Inaug. Diss. Bern.*, 61 p.

SCOTT, C. E., 1920, A preliminary note on the germination of Urophlyctis alfalfae, *Science, N. S.*, **52**: 225–226.

SEAVER, F. J., 1910, Hypocreales, *N. Amer. Fl.*, **3**: 1–56.

———, 1915, Photographs and descriptions of cup fungi, *Mycologia*, **7**: 90–93, *pl. 155–156.*

SERBINOV, I. L., 1907, Organizatsiia i rasvitie nekotorykh gribov Chytridineae Schröter. Materialy k izucheniu flory Rossii XVII, *Scripta Bot. Hort. Imp. Petropol.*, **24**: 1–173, *pl. 1–6.*

SETCHELL, W. A., 1892, An examination of the species of the genus Doassansia Cornu, *Ann. Botany*, **6**: 1–48, *pl. 1–2.*

———, 1910, The genus Sphaerosoma, *Univ. California Publ. Bot.*, **4**: 107–118, *pl. 15.*

SEYFERT, R., 1927, Über Schnallenbildungen im Paarkernmyzel der Brandpilze, *Zeitschr. f. Botanik*, **19**: 577–601, *22 fig.*

SEYNES, J. DE, 1874, Recherches pour servir à l'histoire naturelle des végétaux inférieurs, I. Des Fistulines, [Paris] 72 p., *7 pl.*

SHANTZ, H. L., and R. L. PIEMEISEL, 1917, Fungus fairy rings in eastern Colorado and their effect on vegetation, *Jour. Agr. Res.*, **11**: 191–245. *pl. 10–30.*

SHEAR, C. L., 1907, New species of fungi, *Bull. Torrey. Botan. Club*, **34**: 305–317.

———, 1925, The life history of the Texas root rot fungus Ozonium omnivorum Shear, *Jour. Agr. Res.*, **30**: 475–477, *pl. 1.*

SHEAR, C. L., and B. O. DODGE, 1921, The life history and identity of Patellina Fragariae, *Mycologia*, **13**: 135–170, *pl. 8–10.*

———, 1925, The life history of Pilacre faginea (Fr.) B. & Br., *Jour. Agri. Res.*, **30**: 407–417, *2 pl.*

———, 1927, Life histories and heterothallism of the red bread mold fungi of the Monilia sitophila group, *Jour. Agr. Res.*, **34**: 1019–1042; *pl. 1–4.*

SHEAR, C. L., N. E. STEVENS and R. J. TILLER, 1917, Endothia parasitica and related species, *U. S. Dept. Agr. Bull.*, **380**: 82 p.

SHEAR, C. L., N. E. STEVENS and M. S. WILCOX, 1925, Botryosphaeria and Physalospora in the eastern United States, *Mycologia*, **17**: 98–107, *pl. 9.*

SMITH, A. L., 1921, Lichens [Cambridge], 464 p.

SMITH, G., 1900, The haustoria of the Erysipheae, *Botan. Gaz.*, **29**: 153–184, *pl. 11–12.*

SMITH, R. E., 1900, Botrytis and Sclerotinia, *Botan. Gaz.*, **29**: 369–407, *pl.* 25–27.

SNELL, W. H., 1922, A new Septobasidium on Pinus strobus, *Mycologia*, **14**: 55–60, *pl. 11–13.*

SOLMS-LAUBACH, H., 1886, Penicilliopsis clavariaeformis. Ein neuer javanischer Ascomycet, *Ann. Jard. Botanique Buitenzorg*, **6**: 53–72.

SOPP, O. JOHAN-OLSEN, 1911, Untersuchungen über insektenvertilgende Pilze, [Christiania], *Vid. Selsk. Skr. I math.-nat. Kl.* **1911**[2]: 1–56.

———, 1912, Monographie der Pilzgruppe Penicilium mit besonderer Berücksichtigung der in Norwegen gefundenen Arten, [Christiania], *Vid. Selsk. Skr., math.-nat. Kl.*, **1912**[11]: 1–208, *pl. 1–23.*

STÄGER, R., 1905, Weitere Beiträge zur Biologie des Mutterkorns, *Centralbl. Bact. II Abt.*, **14**: 25–32.

———, 1910, Neue Beobachtungen über das Mutterkorn, *Centralbl. Bact. II Abt.*, **27**: 67–73.

———, 1912, Infektionsverusche mit überwinterten Clavicepskonidien, *Myc. Centralbl.* **1**: 198–201.

———, 1922, Beitrag zur Verbreitungsbiologie der Clavicepssklerotien, *Centralbl. Bact. II Abt.*, **56**: 329–339.

STEINER, J. A., 1908, Die Spezialisation der Alchemillen-bewohnenden Sphaerotheca Humuli, *Centralbl. Bact., II Abt.*, **21**: 677–736.

STEVENS, F. L., 1899, The compound oosphere of Albugo Bliti, *Botan. Gaz.*, **28**: 149–176; 225–245, *pl. 11–15.*

———, 1901, Gametogenesis and fertilization in Albugo, *Botan. Gaz.*, **32**: 77–97; 157–169; 238–261, *pl. 1–4.*

———, 1904, Oogenesis and fertilization in Albugo Ipomoeae-panduranae, *Botan. Gaz.*, **38**: 300–302, *f. 1, 2.*

———, 1927, New tropical fungi, *Mycologia*, **19**: 231–232, *pl. 18–21.*

———, 1927*a*, The Meliolineae, I. *Ann. Myc.*, **25**: 405–469, *pl. 1–2.*

STEVENS, F. L. and A. C., 1903, Mitosis of the primary nucleus in Synchytrium decipiens. *Botan. Gaz.*, **35**: 405–415, *pl. 16–17.*

STEVENS, F. L. and A. G. WEEDON, 1923, Three new myriangiaceous fungi from South America, *Mycologia*, **15**: 197–206, *pl. 18–20.*

STEWART, V. B., 1916, The leaf blotch disease of horse-chestnut, *Phytopathology*, **6**: 5–19, *pl. 2–4.*

STOPPEL, R., 1907, Eremascus fertilis nov. spec., *Flora*, **97**: 332–346, *pl. 11–12.*

STORK, H. E., 1920, Biology of Aleurodiscus, *Amer. Jour. Botany*, **7**: 445–457, *pl. 31–33.*

STREETER, ST. G., 1909, The influence of gravity on the direction of growth of Amanita, *Botan. Gaz.*, **48**: 414–426, *f. 1–13.*

STRELIN, S., 1912, Beiträge zue Biologie und Morphologie der Kuehneola albida (Kühn) Magn. und Uredo Muelleri Schroet., *Myc. Centralbl.*, **1**: 92–96; 131–137.

SVEDELIUS, N., 1921, Einige Bermerkungen über Generationswechsel und Reduktionsteilung, *Ber. Deutsch. Botan. Ges.*, **39**: 178–187.

———, 1927, Alternation of generations in relation to reduction division, *Botan. Gaz.*, **83**: 361–384.

SWINGLE, D. B., 1903, Formation of the spores in the sporangia of Rhizopus nigricans and Phycomyces nitens, *Bull. Bur. Plant Ind.*, **37**: 1–40.

TANDY, G., 1927, The cytology of Pyronema domesticum (Sow.), Sacc. *Ann. Botany*, **41**: 321–325, *pl. 16.*

TAVEL, F. VON, 1886, Beiträge zur Entwickelungsgeschichte der Pyrenomyceten, *Botan. Zeitung.*, **44**: 825–833; 841–846; 857–867; 873–878, *pl. 7.*

———, 1892, Vergleichende Morphologie der Pilze [Jena], 208 p.

TERBY, J., 1923, L'origine de blépharoplaste chez le Plasmodiophora Brassicae, *Bull. Soc. R. Botanique Belqique*, **56**: 48–50.

THAXTER, R., 1888, The Entomophthoreae of the United States, *Mem. Boston Soc. Nat. Hist.*, **4**: 133–201, *pl. 14–21.*

———, 1893, Note on Phallogaster saccatus, *Botan. Gaz.*, **18**: 117–121, *pl. 9.*

———, 1894, Observations on the genus Naegelia of Reinsch, *Botan. Gaz.*, **19**: 49–55, *pl. 5.*

———, 1895, New or peculiar aquatic fungi. I. Monoblepharis, *Botan. Gaz.*, **20**: 433–440; 477–485, *pl. 29.*

———, 1895*a*, New or peculiar American Zygomycetes, I. Dispira, *Botan. Gaz.*, **20**: 513–518, *pl. 34.*

———, 1896, Contribution towards a monograph of the Laboulbeniaceae I, *Mem. Amer. Acad. Arts. Sci.*, **12**: 189–429, *pl. 1–24.*

———, 1897, New or peculiar American Zygomycetes. 2. Syncephalastrum and Syncephalis, *Botan. Gaz.*, **28**: 1–15, *pl. 1–2.*

———, 1908, Contribution towards a monograph of the Laboulbeniaceae II, *Mem. Amer. Acad. Arts Sci.*, **13**: 219–469, *pl. 28–71.*

———, 1914, On certain peculiar fungus-parasites of living insects, *Botan. Gaz.*, **58**: 235–253, *pl. 16–19.*

———, 1914*a*, New or peculiar American Zygomycetes III, Blakeslea, Dissophora, and Haplosporangium, nova genera, *Botan. Gaz.*, **58**: 353–366, *pl. 26–29.*

———, 1917, New Laboulbeniales chiefly dipterophilous American species, *Proc. Amer. Acad. Arts Sci.*, **52**: 649–721.

———, 1920, Second note on certain peculiar fungus-parasites of living insects, *Botan. Gaz.*, **69**: 1–27, *pl. 1–5.*

———, 1922, A revision of the Endogoneae, *Proc. Amer. Acad. Arts Sci.*, **57**: 291–350, *pl. 1–4.*

———, 1922*a*, Note on two remarkable Ascomycetes, *Proc. Amer. Acad. Arts Sci.*, **57**: 425–434, *1 pl.*

———, 1924, Contribution towards a monograph of the Laboulbeniaceae III, *Mem. Amer. Acad. Arts Sci.*, **14**: 313–414, *pl. 1–12.*

———, 1926, IV, *Ibid.*, **15**: 431–580, *pl. 1–24.*

THEISSEN, F., 1909, Xylariaceae austrobrasilienses, *Ann. Myc.*, **7**: 1–18; 141–167.

———, 1911, Die Hypocreaceen von Rio Grande do Sul, *Ann. Myc.*, **9**: 40–73, *pl. 5–7.*

THEISSEN, F., 1912, Fragmenta brasilica IV, nebst Bemerkungen über einige andere Asterina-Arten., *Ann. Myc.*, **10**: 1–32.
———, 1912, Zur Revision der Gattung Dimerosporium, *Beih. Botan. Centralbl. II Abt.*, **29**: 45–73.
———, 1912, Le genre Asterinella, *Broteria, ser. bot.*, **10**: 101–124.
———, 1913, Lembosia Studien, *Ann. Myc.*, **11**: 425–467.
———, 1914, Die Trichothyriaceen, *Beih. Botan. Centralbl. II Abt.*, **32**: 1–16, *pl. 1.*
———, 1914*a*, Über Membranstrukturen bei den Microthyriaceen als Grundlage für den Ausbau der Hemisphaeriales, *Myc. Centralbl.*, **3**: 273–286, *pl. 1.*
———, 1914*b*, Über Polystomella, Microcyclus u. a., *Ann. Myc.*, **12**: 63–75, *pl. 6, 7.*
———, 1914*c*, Trichopeltaceae n. fam. Hemisphaerialium, *Centralbl. Bact. II*, **39**: 625–640, *1 pl.*
———, 1916, Mykologische Abhandlungen I. Zur Phylogenie der Pseudosphaerieen, *Verh. K. Zool. Botan. Ges. Wien.*, **66**: 296–400, *pl. 1.*
———, 1916*a*, Studien über Botryosphaeria, *Ann. Myc.*, **14**: 297–340.
———, 1916*b*, Beiträge zur Systematik der Ascomyceten, *Ann. Myc.*, **14**: 401–439.
———, 1917, Über Tympanopsis und einige andere Gattungstypen, *Ann. Myc.*, **15**: 269–277.
THEISSEN. F., and H. SYDOW, 1915, Die Dothideales *Ann. Myc.*, **13**: 149–746.
———, 1917, Synoptische Tafeln, *Ann. Myc.*, **15**: 389–491.
———, 1918, Vorentwürfe zu den Pseudophaeriales, *Ann. Myc.*, **16**: 1–34.
THOM, C., 1914, Conidium production in Penicillium, *Mycologia*, **6**: 211–215.
THOM, C., and M. B. CHURCH, 1921, Aspergillus flavus, A. Oryzae and associated species, *Amer. Jour. Botany*, **8**: 103–126.
———, 1926, The Aspergilli, Baltimore, 272 p.
THURSTON, H. W., 1923, Intermingling gametophytic and sporophytic mycelium in Gymnosporangium bermudianum, *Botan. Gaz.*, **75**: 225–248, *pl. 12–13.*
TIEGHEM, P. VAN, 1875, Nouvelles recherches sur les mucorinées, *Ann. Sci. Nat. Botanique* 6 *sér.* **1**: 1–174, *pl. 1–4.*
———, 1893, Sur la classification des Basidiomycètes, *Journ. de Botanique* [Morot], **7**: 77–87.
TIEGHEM, P. VAN, and G. LEMMONNIER, 1873, Recherches sur les Mucorinées, *Ann. Sci. Nat. Botanique*, 5 *ser.*, **17**: 261–399, *pl.* 20–25.
TIESENHAUSEN, M., 1912, Beiträge zur Kenntnis der Wasserpilze der Schweiz, *Arch. f. Hydrobiol.*, **7**: 261–308.
TISDALE, W. H., 1919, Physoderma disease of corn, *Jour. Agr. Res.*, **16**: 137–154, *pl. A-B, 10–17.*
TOBLER, F., 1925, Biologie der Flechten [Berlin], 266 p.
TOBLER-WOLFF, G., 1912, Die Synchytrien. Studien zu einer Monographie der Gattung, *Arch. f. Protistenk.*, **28**: 141–238, *pl. 10–13.*
TRANZSCHEL, W., 1910, Die auf der Gattung Euphorbia auftretenden autöcischen Uromyces Arten, *Ann. Myc.*, **8**: 1–35.
TROW, A. H., 1899, Observations on the biology and cytology of a new variety of Achlya americana, *Ann. Botany*, **13**: 131–179, *pl. 8–10.*
———, 1901, Observations on the biology and cytology of Pythium ultimum n. sp., *Ann. Botany*, **15**: 269–312, *pl. 15, 16.*
———, 1904, On fertilization in the Saprolegnieae, *Ann. Botany*, **18**: 541–569, *pl. 34–36.*
TUBEUF, C. VON, 1901, Studien über die Schüttekrankheit der Kiefer, *Arb. Biol. Reichsanst. Forst- u. Landw.*, **2**: 1–160.
———, 1913, Die geweihförmigen Pilzgallen am Lorbeer, *Naturw. Zeitschr. f. Forst- und Landw.*, **11**: 401–407.

VALLORY, J., 1911, Sur la formation du perithèce dans le Chaetomium Kunzeanum Zopf. var. chlorinum Mich., *Comptes Rendus Acad. Sci.* [Paris], **153**: 1012–1014.

VANDENDRIES, R., 1923, Nouvelles recherches sur la sexualité des Basidiomycètes, *Bull. Soc. R. Botanique Belg.*, **56**: 73–97.

———, 1923, Recherches sur le déterminisme sexuel des Basidiomycètes, *Mém. Acad. R. Belg., Cl. Sci.* 2 *sér.*, **5**: 1–98, *8 pl.*

———, 1924, Recherches expérimentales sur la bipolarité sexuelle des Besidiomycètes, *Bull. Soc. R. Botanique Belg.*, **57**: 75–78.

———, 1925, Recherches experimentales prouvant la fixité du sexe dans Coprinus radians Desm., *Bull. Soc. Myc. France*, **41**: 358–374.

———, 1925*a*, Contribution nouvelle à l'étude de la sexualité des Basidiomycètes, *La Cellule*, **35**: 129–155, *1 pl.*

———, 1926, La tetrapolarité sexuelle des Coprins, *Bull. Soc. R. Botanique Belg.*, **58**: 180–186.

VAUGHAN, R. E., 1916, The development of Mycosphaerella pinodes in pure culture, *Phytopathology*, **6**: 103.

VINCENS, F., 1917, Recherches organogéniques sur quelques Hypocréacées, *Thèse* [Paris], 166 p., *3 pl.*

———, 1918, Valeur taxonomique d'une particularité de la structure des ascospores chez les Xylariacées, *Bull. Soc. Myc. France*, **34**: 101–109.

VOSS, W., 1903, Über Schnallen und Fusionen bei den Uredineen, *Ber. Deutsch. Bot. Ges.*, **21**: 366–371, *pl. 19.*

VUILLEMIN, P., 1886, Études biologiques sur les champignons, *Bull. Soc. Sci. Nancy*, 2. *sér.*, **8**: 33–161, *pl. 1–6.*

———, 1887, Sur le polymorphisme des Pézizés, *Comptes Rendus Ass. Franç. Avanc. Sci.*, **1886**: 491–497, *pl. 10.*

———, 1893, Remarques sur les affinités des Basidiomycétes, *Jour. de Botanique* [Morot], **7**: 164–174.

———, 1897, Les Hypostomacées, nouvelle famille de champignons parasites, *Bull. Soc. Sci. Nancy*, *sér.* 2, **14**: 15–67 [1896].

———, 1901, Développement des azygospore chez les Entomophthorées, *Comptes Rendus Ass. Franç. Avanc. Sci.*, **1900**[2]: 670–685, *pl. 6.*

———, 1902, Les cephalidées, *Bull. Séanc. Soc. Sci. Nancy 3 sér.*, **3**: 21–83.

———, 1903, Importance taxonomique de l'appareil zygosporé des Mucorinées, *Bull. Soc. Myc. France*, **19**: 106–118.

———, 1904, Recherches morphologiques et morphogéniques sur la membrane des zygospores, *Ann. Myc.*, **2**: 483–506, *pl. 8–11.*

———, 1904, Le Spinellus chalybeus (Dozy & Molkenboerg) Vuillemin et la série des Spinellées, *Ann. Myc.*, **2**: 61–69, *pl 4.*

———, 1905, Identité des genres Meria et Hartigiella, *Ann. Myc.*, **3**: 340–343, *8 fig.*

———, 1907, Les bases actuelles de la systématique en mycologie, *Progr. Rei Botan.*, **2**: 1–170.

———, 1912, Les champignons [Paris], 420 p.

WAGER, H., 1896, On the structure and reproduction of Cystopus candidus Lév., *Ann. Botany*, **10**: 295–342, *pl. 15–16.*

———, 1900, On the fertilization of Peronospora parasitica, *Ann. Botany*, **14**: 263–279, *pl. 16.*

———, 1913, The life-history and cytology of Polyphagus Euglenae, *Ann. Botany*, **27**: 173–202, *pl. 16–19.*

WAKEFIELD, E. M., 1909, Über die Bedingungen der Fruchtkörperbildung sowie das Auftreten fertiler und steriler Stämme bei Hymenomyceten, *Naturw. Zeitschr. f. Forst-u. Landw.*, **7**: 521–551, *1 pl.*

WALKER, L. B., 1919, Development of Pluteus admirabilis and Tubaria furfuracea, *Botan. Gaz.*, **68**: 1–21. *f. 1–8, pl. 1–5.*

———, 1920, Development of Cyathus fascicularis, C. striatus and Crucibulum vulgare, *Botan. Gaz.*, **70**: 1–24, *pl. 1–6.*

———, 1922, The forceful ejection of the glebal mass by Sphaerobolus, *Proc. Nebraska Acad. Sci.*, **10**: 23–25.

———, 1923, Some observations on the development of Endogone malleola Hark., *Mycologia*, **15**: 245–257, *pl. 26–27.*

———, 1927, Development and mechanism of discharge in Sphaerobolus iowensis n. sp. and S. stellatus Tode, *Jour. Elisha Mitchell Sci. Soc.*, **62**: 151–178, *pl. 16–25.*

WALKER, L. B., and E. N. ANDERSEN, 1925, Relation of glycogen to spore ejection, *Mycologia*, **17**: 154–159, *pl. 18.*

WARD, H. M., 1899, Onygena equina Willd., a horn destroying fungus, *Phil. Trans. R. Soc. London B.*, **191**: 269–291, *pl. 21–24.*

WEBER, G. F., 1922–1923, Septoria diseases of cereals, *Phytopathology*, **12**: 448–470, 537–585, *pl. 23–36;* **13**: 1–23.

WEESE, J., 1911, Zur Kenntnis des Erregers der Krebskrankheit an den Obst-und Laubholzbäumen, *Zeit. Landw. Versuchswesen in Österreich*, **14**: 872–885, *pl. 1.*

———, 1914, Zur Kenntnis der Gattung Calonectria, *Myk. Centralbl.* **4**: 121–132; 177–187.

———, 1915, Hypocreaceenstudien I, *Centralbl. Bact. II Abt.*, **42**: 587–613.

———, 1916–1919, Beitrage zur Kenntnis der Hypocreaceen I, II *Sitzungsber. Akad Wiss. Wien Math. Naturw. Kl. Abt. 1*, **125**: 465–575, *pl. 13;* **128**: 693–754, *1 pl.*

———, 1917, Studien uber Nectriaceen III, *Zeitschr. f. Garungsphys.*, **6**: 28–46.

———, 1919, Über die Gattungen Melanops Nitschke und Thuemenia Rehm, *Ber. Deutsch. Botan. Ges.*, **37**: 83–96.

———, 1919, Mykologische und phytopathologischen Mitteilungen, *Ber. Deutsch Botan. Ges.*, **37**: 520–527, *pl. 8.*

———, 1920, Beitrag zur Morphologie und Systematik einiger Auriculariineengattungen, *Ber. Deutsch. Botan. Ges.*, [1919], **37**: 512–519.

WEHMER, C., 1901, Die Pilzgattung Aspergillus, *Mem. Soc. Phys. Nat. Genève*, **33**[4]: 1–157, *pl. 1–5.*

———, 1907, Mucoraceengärungen in *Lafar, Handb. Techn. Mycol.*, **4**: 455–528.

———, 1914, Coremium silvaticum n. sp. nebst Bemerkungen zur Systematik der Gattung Penicillium, *Ber. Deutsch. Botan. Ges.*, **32**: 373–384.

WEHMEYER, L. E., 1923, The imperfect stage of some higher Pyrenomycestes obtained in culture, *Papers Michigan Acad. Sci. Arts Letters*, **3**: 245–266.

———, 1924, The perfect stage of the Valsaceae in culture and the hypothesis of sexual strains in this group, *Papers Michigan Acad. Sci. Arts Letters*, **4**: 395–412.

———, 1925, Cultural life histories of certain species of Eutypella, Diatrypella and ——Cryptovalsa, *Papers Michigan Acad. Sci. Arts Letters* **5**: 179–194.

———, 1926, A biologic and phylogenetic study of the stromatic Sphaeriales, *Amer. Jour. Botany*, **13**: 575–645.

———, 1926*a*, Further cultural life histories of the stromatic Sphaeriales, *Amer. Jour. Botany*, **13**: 231–247, *pl. 12–15.*

———, 1928, Cultural life histories of Diaporthe, III, *Papers Michigan Acad. Sci.*, **7**: [in Press].

WEIMER, J. L., 1920, Some observations on the spore discharge of Pleurage curvicolla, *Amer. Jour. Botany*, **7**: 75–77.

WEIR, J. R., 1911, Untersuchungen über die Gattung Coprinus, *Flora*, **103**: 263–320.

———, 1912, A short review of the characteristics and cytological phenomena of the Uredineae, *New Phytologist*, **11**: 129–139.

WEIR, J. R., 1917, Sparassis radicata, an undescribed fungus on the roots of conifers, *Phytopathology*, **7**: 166–177.

WELCH, D. S., 1926, A monographic study of the genus Cucurbitaria in North America, *Mycologia*, **18**: 51–86, *pl. 7–8.*

WELSFORD, E. J., 1907, Fertilization in Ascobolus furfuraceus Pers., *New Phytologist*, **6**: 156–160, *pl. 4.*

———, 1915, Nuclear migrations in Phragmidium violaceum, *Ann. Botany*, **29**: 293–298, *pl. 16.*

WERTH, E., and K. LUDWIGS, 1912, Zur Sporenbildung bei Rost und Brandpilzen, *Ber. Deutsch Botan. Ges.*, **30**: 522–528, *pl. 15.*

WESTLING, R., 1909, Byssochlamys nivea en förening slänk mellan-familijerna Gymnoascaceae och Endomycetaceae, *Svensk Botan. Tidskr.*, **3**: 125–137, *pl. 4.*

———, 1911, Über die grünen Spezies der Gattung Penicillium, *Ark. Botanik*, **11**: 1–156.

WESTON, W. H., 1918, The development of Thraustotheca a peculiar water-mould, *Ann. Botany*, **32**: 155–173, *pl. 4, 5.*

———, 1919, Repeated zoospore emergence in Dictyuchus, *Botan. Gaz.*, **68**: 287–296, *pl. 23.*

WETTSTEIN, F., 1921, Das Vorkommen von Chitin und seine Verwertung als systematischphylogenetisches Merkmal im Pflanzenreich, *Sitzungsber. Akad. Wiss. Wien, Math. Naturw. Kl. Abt. I*, **130**: 3–20.

WILSON, G. W., 1914, Studies in North American Peronosporales VI, *Mycologia*, **6**: 192–210, *pl. 135–136.*

WILSON, M., 1915, The life history and cytology of Tuburcinia primulicola Rostrup, *British Ass. Adv. Sci. Rept.*, **1915**: 730–731.

WINGARD, S. A., 1925, Studies on the pathogenicity, morphology and cytology of Nematospora Phaseoli, *Bull. Torrey Botan. Club*, **52**: 249–290.

WINGE, Ö., 1911, Encore la Sphaerotheca Castagnei, *Bull. Soc. Myc. France*, **27**: 211–219, *pl. 7–8.*

———, 1913, Cytological studies in the Plasmodiophoracae, *Ark. Botanik*, **12**^{9}: 1–39, *pl. 1–3.*

WINKLER, H., 1908, Über Parthenogenesis und Apogamie im Pflanzenreich, *Progr. Rei Botan.*, **2**: 293–454.

WINTER, G., 1887, Ascomyceten, [Rabenhorst] *Krypt. fl. Deutschl. I*, **2**: 928 + 48 p.

WOLF, F. A., 1912, Spore formation in Podospora anserina, *Ann. Myc.*, **10**: 60–64.

———, 1917, A squash disease caused by Choanephora Cucurbitarum, *Jour. Agr. Res.*, **8**: 319–327, *pl. 85–87.*

WOLFF, G. P., 1905, Beiträge zur Entwicklungsgeschichte der Flechtenapothecien, *Flora*, **95**: 31–57.

WOLLENWEBER, H. W., 1914, Indentification of species of Fusarium occurring on the sweet potato Ipomoea batatas, *Jour. Agr. Res.*, **2**: 251–286, *pl. 12–16.*

———, 1924, Pyrenomycetenstudien, *Angew. Botanik*, **6**: 300–313.

WORONIKHIN, N. N., 1914, Plectodiscella piri, der Vertréter einer neuen Ascomyceten-Gruppe, *Myc. Centralbl.*, **4**: 225–233.

WORONIN, M., 1864, Zur. Entwicklungsgeschichte des Ascobolus pulcherrimus und einiger Pezizen, *Abh. Senckenberg. Naturf. Ges.*, **5**: 333–344, *pl. 39–42.*

———, 1867, Exobasidium Vacinii, *Ber. über die Verh. Naturforsch. Ges. Freiburg*, **4**: 397–416, *3 pl.*

———, 1878, Plasmodiophora brassicae, Urheber der Kohlpflanzen-Hernie, *Jahrb. Wiss. Botanik*, **11**: 548–574, pl. *29–34.*

———, 1881, Beitrag zur Kenntnis der Ustilagineen. *Abh. Senckenberg. Naturf. Ges.*, **12**: 559–591, *pl. 1–4* [also cited as Bary and Woronin, *Beitr. Morphol. Physiol. Pilze* 5].

WORONIN, M., 1888, Über die Sclerotiniakrankheit der Vaccinieenbeeren, *Mém. Acad. Imp. Sci. Pétersbourg* 7. *sér.*, **36**: *Nr.* 6, 1–49 p.

———, 1904, Beitrag zur Kenntnis der Monoblepharideen, *Mem. Acad. Imp. Sci. Pétersbourg 8. sér. Cl. Phys.*, **16**: 1–24.

WOYCICKI, Z., 1904, Einige neue Beiträge zur Entwicklungsgeschichte von Basidiobolus ranarum Eidam, *Flora*, **93**: 87–97, *pl. 4.*

———, 1907, Einige erklärende Worte zur Kritik meiner abhandlung: "Neue Beiträge zur Entwicklungsgeschichte von Basidiobolus ranarum Eid." in den Vorlesungen uber botanische Stammesgeschichte von Prof. Lotsy, *Ber. Deutsch. Botan. Ges.*, **25**: 581–582.

———, 1927, Über die Zygotenbilding bei Basidiobolus ranarum Eidam II, *Flora*, **122**: 159–166, *pl. 1–2.*

YATES, H. S., 1916, The comparative histology of certain Californian Boletaceae, *Univ. California Publ. Botany*, **6**: 221–274, *pl. 21–25.*

ZELLER, S. M., 1914, The development of Stropharia ambigua, *Mycologia*, **6**: 139–145, *pl. 124–125.*

———, 1914, The development of the carpophores of Ceriomyces Zelleri, *Mycologia*, **6**: 235–239, *pl. 140–141.*

———, 1915, Notes on Cryptoporus volvatus, *Mycologia*, **7**: 121–125, *pl. 159.*

———, 1916, Lenzites saepiaria Fries with special reference to enzyme activity, *Ann. Mo. Bot. Gard.*, **3**: 439–514, *pl. 8–9.*

ZELLER, S. M., and C. W. DODGE, 1918, Rhizopogon in North America, *Ann. Mo. Bot. Gard.*, **5**: 1–36, *pl. 1–3.*

———, 1918, Gautieria in North America, *Ann. Mo. Bot. Gard.*, **5**: 133–142, *pl. 9.*

———, 1919, Arcangeliella, Gymnomyces and Macowanites in North America, *Ann. Mo. Bot. Gard.*, **6**: 49–59.

———, 1924, Leucogaster and Leucophlebs in North America, *Ann. Mo. Bot. Gard.*, **11**: 389–410, *pl. 11.*

ZELLNER, J., 1907, Chemie der höhern Pilze [Leipzig], 257 p.

ZIKES, H., 1922, Über die Perithezienbildung bei Aspergillus Oryzae, *Centralbl. Bakt. II*, **56**: 339–343.

ZILLIG, H., 1921, Über spezialisierte Formen bei Antherenbrand, Ustilago violacea (Pers.) Fuck., *Centralbl. Bact. II Abt.*, **53**: 33–74.

ZOPF, W., 1878, Die Conidienfrüchte von Fumago, *Nov. Act. K. Leopol. Carol. Deutsch. Akad. Naturf. Halle*, **40**: 257–329, *pl. 19–26.*

———, 1883, Zur Kenntnis der anatomischen Anpassung der Pilzfrüchte an die Funktion der Sporenentleerung, *Zeitschr. f. Naturwiss.*, **56**: 539–574, *pl. 6–8.*

———, 1885, Zur Kenntnis der Phycomyceten I, *Nov. Act. K. Leop. Carol. Deutsch. Akad. Naturf. Halle*, **47**: 143–236, *pl. 12–21.*

———, 1887, Über einige niedere Algenpilze Phycomyceten und eine neue methode ihre keime aus dem Wasser zu isolieren, *Abh. Naturf. Ges. Halle*, **17**: 79–107, *pl. 1–2.*

———, 1888, Zur Kenntnis der Infektionskrankheiten niederer Tiere und Pflanzen, *Nov. Act. K. Leop. Carol. Deutsch. Akad. Naturf. Halle*, **52**: 313–376, *pl. 17–23.*

———, 1890, Die Pilze, [Schenk] *Handb. d. Botanik*, **4**: 271–755.

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