Introduction to the study of fungi : their organography, classification and distribution, for the use of collectors / by M.C. Cooke.

Contributors

Cooke, M. C. 1825-1914. Royal College of Physicians of Edinburgh

Publication/Creation

London : A. and C. Black, 1895.

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THE STUDY OF FUNGI



INTRODUCTION

TO

THE STUDY OF FUNGI

THEIR ORGANOGRAPHY, CLASSIFICATION, AND DISTRIBUTION

FOR THE USE OF COLLECTORS

BY

M. C. COOKE, M.A., LL.D., A.L.S.

AUTHOR OF

"fungi: their nature, uses, etc."; "handbook of british fungi"; "illustrations of british fungi"; "microscopic fungi"; "british edible fungi"; "handbook of australian fungi," etc. etc.



LONDON ADAM AND CHARLES BLACK 1895



PREFACE

THE Introduction to Cryptogamic Botany, published by Berkeley in 1857, was for a long time the only volume, in English, which could introduce the inquiring student to a systematic knowledge of Fungi. Later on, this work was discovered to be insufficient, inasmuch as it was more suited to the requirements of an advanced student than an inquirer; so that the field was left open for a more popular and elementary work, which, under the title of Fungi: their Nature, Influence, and Uses, appeared in 1875, subsequently passing through several editions. The rapid advance in knowledge of the life-history and development of these organisms during the past ten years, and especially the large scheme of classification carried out by Professor Saccardo, made it essential that, in order to keep pace with the times, a guide and introduction should be prepared and published for the use of students, which, whilst not superseding the volume of 1875 as a popular instructor, should treat the subject more after the manner of a text-book, adapted to the illustration of recent discoveries, and an explanation of the methods of classification. The following pages are the result of an effort to supply an acknowledged want, which I have executed under the impression that it is probably my last contribution of any importance to British Mycology.

For many of the illustrations the publishers and myself duly acknowledge the kindness with which they have been placed at our disposal by the publishers of the works from

whence they are taken. A large number of the woodcuts will be recognised as formerly belonging to my *Handbook of* B_{T} *itish Fungi*, the use of which has now been granted by Messrs. Swan Sonnenschein and Co. We are also under obligations to the publishing committee of the Society for Promoting Christian Knowledge, to the proprietors of the *Gardener's Chronicle*, to Messrs. Kegan Paul, Trench, Trubner, and Co., Messrs. Macmillan and Co., and Messrs. Chatto and Windus; for which they will please accept our acknowledgments.

Beyond this brief prelude I need not advance, as, under any circumstances, readers would prefer taking their evidence from the chapters which follow than from any professions or explanations in a preface. To the student who seeks for assistance I have offered all that I had to give, in the hope that it will be found sufficient for his need.

M. C. COOKE.

LONDON, 1895.

CONTENTS

CHAPTER I

PAGE

1

INTRODUCTION

PART I

ORGANOGRAPHY

CHAPTER II

CHAPTER III

CHAPTER IV

CHAPTER V

CHAPTER VI

CHAPTER VII

PAGE

DICHOCARPISM .	·	*/	:	•		٠	64
	CHA	PTER	e viii				
SAPROPHYTES AND PARA	SITES						73
	CHA	PTE	R IX				
Constituents .							84
	Ρ.	ART	II				
C	LASS	IFIC	ATIO	N			
	CH	APTE	RX				
Fungi in General							95
	СНА	PTEI	D VI				
NAKED-SPORED FUNGI-							119
	OT L	Dana					
HYMENOMYCETES .		PTER					100
TIMENOMICETES .	·		·	·	•	•	120
	CHAI	PTER	XIII				
PUFF-BALL FUNGI-GAS	TROMYCE	TES	-	•	•	•	149
	CHAI	PTER	XIV				
Ascigerous Fungi-Asc	OMYCETH	s		•	•		164
	CHA	PTER	xv				
DISCOID FUNGI-DISCOM	YCETES						173

v

	CONTE	NTS			ix
	CHAPTEI	R XVI			
SUBTERRANEAN FUNGI-	-TUBERACEAE		•		. 189
	CHAPTER	R XVII			
Capsular Fungi—Pyr	RENOMYCETES	•			. 197
	CHAPTER	XVIII			
GAPING FUNGI—HYSTE	TRIACEAE .				. 222
	CHAPTER	R XIX			
Conjugating Fungi-	Phycomycetes	•	•		. 227
	CHAPTEI				
Rust Fungi-Uredine	AE .	•	•	1	. 242
	CHAPTER	XXI			
Smut Fungi—Ustilagi	NES .				. 251
	CHAPTER	XXII			
MPERFECT CAPSULAR F	UNGI—SPHAERO	PSIDEAE	•		. 259
	CHAPTER	XXIII			
IOULDS-HYPHOMYCETE	8.	•	•	·	. 277
	CHAPTER	XXIV			
licrobes-Schizomycet	ES AND SACCHA	ROMYCET	res		. 290
	CHAPTER	XXV			
LIME FUNGI-MYXOMYC	VETES .				. 304

PART III

DISTRIBUTION

	CHA	PTER	XXV	[-		PAGE	
CENSUS OF FUNGI		•		;	•		
	CHA	PTER	XXVI	I			
GEOGRAPHICAL DIST	RIBUTION	•	•			. 324	
	CHA	PTER	XXVI	II			
Appendix on Coll	ECTING			•		• . 345	
GLOSSARY .	1					. 353	
INDEX	ζ.,				•	. 358	

CHAPTER I

INTRODUCTION

THE student will expect to find in an Introduction to the study of any subject some definition and delimitation of that subject -a task difficult in all cases to accomplish with brevity, and within the compass of a technical description, but one of increased difficulty when the subject is so extensive and complicated as Fungi. In past times definitions have been hazarded which appeared at the time to be incontestable and complete, but within a short period they became insufficient. That they are plants of a low organisation must be conceded, and also that they belong to the lowest section, or the Cryptogamia, in which the reproductive organs are more or less concealed; but the old characteristics of Algae as cellular plants subsisting in water; of Lichens as subsisting in air, and not upon the matrix on which they flourish; and, finally, of Fungi, which derived their sustenance from the matrix, have had to be discarded as insufficient. It is now known that aquatic Fungi are not an impossibility, that Algae may grow in a damp atmosphere, and that some portion of the substance of Lichens may be derived from their matrix. Seeing the difficulty of obtaining positive characters, negative ones have been tried; but these again have failed to give satisfaction. In one of the most recent works which has attempted to deal with this difficulty we meet with the following as one of the "leading characters." It is to the effect that " Chlorophyll, the green colouring matter so general in the vegetable kingdom, is entirely absent from fungi."1 Admitting this to be true, may it not be maintained that there

¹ Massee, British Fungi (1891), p. 1.

are probably some lichens or some algae in which true chlorophyll is not present?

But speaking of them as a whole, we are justified in saying of Fungi that they are "cryptogams without chlorophyll," and in this we shall embody the most important characters of the group "—a general definition which may be accepted without reservation. Except for one or two small families, we could add also "without determinate sexuality."

Previous to this, Berkeley had pointed out that the definition was imperfect which described Fungi as "deriving nourishment by means of a mycelium from the matrix, and never producing from their component threads green bodies resembling chlorophyll,"¹ for, he goes on to observe, "it is true that a few Algae, such as Botrydium, do probably imbibe something from the soil by means of their rootlets, which can scarcely be mere holdfasts"; and again, "When we examine Fungi more closely, we shall have reason to believe that there are exceptions here also as to their deriving nutriment from their matrix. I have, for instance, found a Cyphella on the hardest gravel stones, where the fine mycelioid threads, by which it was attached, could not possibly derive any nutriment except from matters conveyed to it by the air or falling To the latter portion of the paragraph, giving the moisture." negative character of the absence of chlorophyll, Berkeley, however, gives his adhesion.

A logical definition, therefore, so commonly fails, that we shall excuse ourselves from attempting a new one, simply indicating a few points to be borne in mind whilst perusing the following pages, from whence alone a general idea can be obtained of such a polymorphous group. Lindley divided all the Cryptogamic plants into two sections, the *Acrogens*, growing at the summit, including the Ferns, Mosses, and their allies, and the *Thallogens*, which embraced Algae, Fungi, and Lichens. Hence we conclude that Fungi are not only Cryptogams, but of that section in which there is no true root or distinct stem with foliaceous appendages. Although the Rev. M. J. Berkeley was, in the main, responsible for Lindley's classification of the Cryptogams, it is out of date and inapplicable in the present

¹ Introduction to Cryptogamic Botany, p. 235.

INTRODUCTION

day, when other and improved methods have been brought into use. Instead of the term *Thallogens* for the cellular Cryptogamia, it would be preferable to call them *Thallophytes*, and, for the rest, *Bryophytes* would include Mosses and their allies, whilst *Pteridophytes* would be represented by the Ferns.

Thallophytes, in a general sense, which will be sufficient for practical purposes, consist of those plants which grow in water, and obtain their sustenance therefrom, commonly known as Algae; and those which flourish in the air, being sustained by the decomposition of the matrix on which they flourish, as Fungi; or drawing their sustenance from the air, and rarely, or but slightly, from the matrix, as in Lichens. Here again a negative feature may be interposed with advantage, to the effect that Lichens are not of a fleshy or putrescent, but of a dry and leathery consistence, whereas in the bulk of Fungi the substance is, either entirely or in the early stage, soft and fleshy, becoming indurated or putrescent with age. The distinctions between Algae and Fungi will never cause any practical difficulty, because the Saprolegnieae, which are aquatic, and approach Algae most nearly in habit, derive their sustenance from the matrix on which they are parasitic by means of penetrating mycelial threads, whereas Algae are simply attached by root-like or sucker-like extensions to the matrix, from which nothing is absorbed. The relations between Fungi and Lichens are much more intimate, and in extreme cases approach each other so closely as to be distinguished with difficulty even by experts. Whole genera are still claimed by mycologists on the one hand, and by lichenologists on the other. Still it must be remembered that these are extreme cases, and that amongst the larger Fungi, especially in the great group of Hymenomycetal Fungi, there is but little suggestion of Lichen affinity except in such genera as Cora, Dictyonema, Pavonia, etc. Another exceptional case may be found in the Nostoes, which are Algae, simulating or so closely resembling Tremella, a genus of Fungi, that microscopical examination may be necessary for their discrimination.

Habitat may in some cases serve to indicate the character of the Thallophyte. For instance, all the parasites on living leaves which are not of insect origin are Fungi, such as the

4

smuts and rusts which are so destructive to crops. There are often to be seen discoloured spots upon living leaves which cannot be attributed either to insects or Fungi. It is a common mistake with novices to infer that all leaf spots are necessarily caused by parasitic Fungi. Again, all the fixed or vegetable parasites on insects are Fungi, whether moulds or the larger club-shaped species of Cordyceps. Another caution becomes necessary lest the pollinidia of Orchids, which are sometimes seen temporarily attached to living insects, should be confounded with true parasites. Putrescent vegetable, and sometimes animal substances, give rise to Fungi, but dead wood and the bark of trees may also support Lichens as well as the living bark, on which Fungi are rarely found, except in cases of incipient decay. No difficulty need be anticipated in respect to Thallophytes found growing upon the ground, inasmuch as the Lichens which have a terrestrial habit would scarcely be confounded with Fungi at any time, but especially after the perusal of succeeding chapters on the details of structure in the several orders. It should be understood that the abovenamed distinctions are not so much of scientific value as they may be useful as guides to collectors.

The mycelium of Fungi is so general, although at times nearly obsolete, that it must be regarded as somewhat analogous to the thallus of Lichens, but not to be confounded therewith. In the Agarics this mycelium is commonly termed the "spawn," and consists of delicate threads, which traverse the soil or the rotten wood upon which the Fungus is grown. In some instances a strong mycelium is developed, but no perfect Fungus is produced upon it. An instance may be found in the substance called Xylostroma giganteum, which forms thick sheets like leather, destructive of wood of solid texture. It is doubtless a degraded form of wood-destroying Hymenomycete.¹ The moulds and the mucors produce at first decumbent barren threads, which constitute the mycelium out of which subsequently the fertile threads arise. In the "rusts" or Uredines the cushion-like base of the pustules is surrounded by the delicate threads of mycelium. Going back to its origin, we discover that the initial spore, or spores, upon germination pro-

¹ See next chapter, p. 10.

INTRODUCTION

duces a delicate thread which, either directly or indirectly, originates the mycelium upon which the Fungus of the new generation is developed. In the Agarics it is held that a large number of spores germinate, and produce the mycelium from which a single individual or a cluster of young Agarics are evolved. In some instances the mycelium is undoubtedly perennial, and produces a crop of Agarics in successive years, but much remains still to be known of the life-history of the Agarics in the interval between the maturity of the spore and the first evidence of the genesis of a new plant.¹ In some of the smut Fungi the germinating spore produces a thread which develops secondary spores, and these in their turn produce tertiary spores before the true mycelium-forming spores are developed. In the Uredines the earliest spore-forms, called "pro-mycelial spores," are produced from the germinating threads of the latest spore-forms or teleutospores, which in turn give rise to the mycelial threads² that enter and form a new mycelium within the tissues of the invaded host-plant. In the Erysiphei the mycelium forms an external coating on the surface of the living leaves, producing at first conidia, and ultimately the perithecia or spore-capsules of the perfect Fungus. Indeed, as a rule, the mycelium represents the vegetative system of the Fungus upon which, under varied forms, the reproductive organs with their appendages are produced. The universality of this mycelium in Fungi was formerly held to be as certain an indication of distinction between a Fungus and a Lichen as the production of a thallus was then held to be a sufficient distinction between a Lichen and a Fungus. In later times it has come to be understood that the hyphal elements in Lichens and Fungi are virtually the same.

¹ In this connection may be consulted Brefeld's researches into the life-history of *Coprinus stereorarius*. ² See post, chap. xx.

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PART I

ORGANOGRAPHY



CHAPTER II

MYCELIUM

In such an immense group as the present, including almost an infinite variety of form, it is extremely difficult to generalise, even the morphology, beyond that of the mycelium, which represents the vegetative system, the carpophore, which supports the fructification, and, finally, the fructification itself, with the organs associated therewith. This, in fact, reduces the whole scheme of structure to its lowest terms, that of the vegetative system and the reproductive, since the carpophore is but a development of the vegetative, and a link between that and the fructification which it is intended ultimately to bear. The details of the varied modifications, which are to accomplish the two purposes of growth and rejuvenescence, can only be described under the great primary divisions of Fungi, where both vegetation and reproduction conform to some definite type. As a whole, the organisms which are associated together under the common denomination of Fungi are the most protean and polymorphic in the entire vegetable kingdom, and present great difficulties in the way of generalisation.

If we gather a mushroom from a mushroom bed, as usually cultivated, we shall discover, if we remove it carefully, that the stem, which represents in this instance the carpophore, or fruit-bearer, is attached to the soil by a mass of delicate white hyphae, or threads, which are the mycelium, or spawn. And if we remove the soil anywhere, we shall find that it is permeated in all directions with these white threads. The artificial "bricks," or spawn, which were employed in the construction of the bed, consisted of this mycelium in a quiescent condition, and by supplying sufficient moisture and

heat, with a suitable matrix, the filaments of this mycelium have been revivified, and by a profuse and rapid growth they have spread over, and penetrated the whole of the soil of which the mushroom bed is composed, and constitute the vegetative system of the mushrooms which afterwards appear on the surface. This mycelium represents an important element in the morphology of all Fungi. It is rarely reduced to such small proportions as not to be recognised, but, practically, it is possibly never wholly absent. We may start, therefore, with what we may regard as an essential attribute of Fungi, and the representative of the purely vegetative system. Whereever we see a Fungus of the mushroom type, whether we please to call it a mushroom or a toadstool, we may find the mycelium in the soil from which it springs. In the autumn, if we stir up and turn over any clump of dead leaves or other decaying vegetable matter in a damp situation, we shall be sure to find a profusion of this mycelium, even though no perfect Fungus makes its appearance, and it is at work on every dead stump and every fragment of rotten wood.

Mycelium consists of hyphae or threads, usually septate, sometimes simple, but mostly branched, increasing by growth at the extremities, and gregarious, so as to form reticulated interwoven masses, either in a thin network or a densely-felted In a certain sense they are analogous to the roots of mass. flowering plants, and, like them, draw moisture and inorganic constituents from the soil or other matrix on which they may be developed. It is another axiom with Fungi that, by means of the mycelium, they derive their sustenance from the matrix on which they grow. It cannot be doubted that the growing points of the mycelium possess the power of penetration by the production of a ferment, since they are capable of penetrating the hardest wood, disintegrating the cells, and reducing The ordinary mycelium found amongst dead it to powder. leaves has a power of disintegration, and soon reduces them, as well as twigs and stems, to a condition of humus; but the progress of mycelium in a dead trunk is quite as definite and Who can doubt the disintegrating power of the certain. mycelium of the "dry rot," and it must be borne in mind that it is the mycelium in this instance which works the

MYCELIUM

mischief. The hyphae forming this vegetative system may be immersed, and probably are so in the majority of instances, but they may also form a stratum on the surface, and adhereby haustoria or suckers, which are short branches designated for the purpose, or for that combined with the absorption of nutriment. The hyphae when young have colourless cell walls, but as they grow older the walls thicken and acquire colour, sometimes with an appearance of stratification. In some

cases cross branches anastomose, or form clamp connections (Fig. 1). Gardeners are well aware that immense masses of white mycelium are sometimes met with in turning over the soil. These mark the site of an old tree when part of the stump or dead roots have been left to rot in the ground. Numerous instances are on record in which trees or shrubs, when planted in soil overrun in this manner with mycelium, have been killed, and when taken up the roots found to be enveloped in mycelium. Practical men are quite aware that this has occurred over



FIG. 1. — Clamp connections. After De Bary.

and over again, and yet some theorists contend that it is not possible, because the mycelium is a saprophyte, that is to say, flourishes upon dead organic matter, and not upon living tissues. Observation has nevertheless decided that in some instances a saprophyte may become parasitical, and a parasite may acquire the habits of a saprophyte. The instances may not be common, but are not impossible. Against theory we are prepared to contend, from experience, that we have seen plants killed, after planting in a soil overrun with mycelium, from no other assignable cause, and afterwards dug up with the roots enveloped in mycelium.

It has been stated above that mycelium is usually colourless, and it is generally so with the Basidiomycetes, but there may be exceptions, as in *Corticium sanguineum*, with its mycelium of a blood red, in *Elaphomyces Leveillei*, of a yellowish green, in *Chlorosplenium aeruginosum*, of a verdigris green, and in many of the *Dematiaei*, of a dark brown, or almost black. And so also it may differ considerably in quantity, from a few scattered threads to a dense matted felt. Even in this country

II

it sometimes forms thick laminae many inches broad in old trunks, but in warmer countries it develops into a spongy mass, called *Xylostroma* in past times. These masses will fill up holes in a log nearly as thick as the wrist, and a foot or two in length, or they will spread in layers of an inch in thickness, a foot in breadth, and several feet long. The whole mass is made up of interwoven threads, almost as dense as cork when felted together, but wholly barren, so that it is uncertain whether they are the mycelium of a Polyporus or an Agaric. Having been furnished with a redundant supply of nutriment, they never advance beyond the vegetative stage. In the case of entomogenous Fungi, the mycelium will replace the whole of the tissues, even to the legs and feet, so as to form a complete cast of the insect, of which only the dermal covering remains unchanged. In such genera as Cordyceps and Empusa the filamentous structure is only seen in the earliest stage; this soon gives way to a compact granular mass. The mycelium of the Mucedines, or moulds, when abundantly supplied with moisture, develop rapidly and vigorously, but do not proceed with the fructification whilst the nutriment supplied is abnor-The conidial stage of the *Erysiphei* will furnish mally great. examples of a thin superficial mycelium adhering by haustoria. In these cases a thin white web runs over the surface of living leaves, as in the vine mildew, and a mildew on the leaves of the maple, but it does not penetrate deeply into the tissues of its host, which it injures by choking up the stomata. Another superficial mycelium is that of Fumago, which forms black patches on the leaves of the lime and other trees, being especially vigorous on those subject to honey-dew. In the sphaerialike or capsular Fungi, the mycelium is confined, usually, to a few delicate threads at the base of the perithecia, but there are exceptions to this in some superficial species, where a subiculum or conidia-bearing mycelium is present.

Another form assumed by mycelia is that condition which has long been known under the name of Rhizomorpha, when it was suspected to be an independent Fungus, although no form of fruit had been discovered. It is now admitted that the several species are only the vegetative condition of other Fungi. One kind may be seen running between the bark and wood of

MYCELIUM

dead trunks in long brown or black cords, as thick as whipcord, flexible, but firm, and either branched or joined by cross connectives of the same substance, into a coarse network. These long cords may be many feet in length, and whitish internally, with a dark-coloured outer coat or skin. The tips of the growing branches are paler. This peculiar growth is very common in mines and other dark places, and glows sometimes with a phosphorescent light. Tulasne examined some specimens with a view to the discovery of the cause of their luminosity, of which Humboldt, amongst others, had given such an elaborate account. He found that all the young branches brightened with a uniform phosphoric light the whole of their length, and also the surface of some of the older branches. The latter when split open were dull, but after exposure for a time to the air they also became luminous. By keeping them moist, they preserved their phosphorescence for several days. He also states that branches which had been dried for more than a month, when plunged into water, revived, and began to vegetate afresh, in a few days, by sending forth numerous branches, but they were only luminous on the surface of the new parts. One of our commonest Agarics, to be found on nearly every rotten stump, Agaricus melleus, is credited with being the complete development of one of the species of Rhizomorpha, which may be stated in this way-the cord-like Rhizomorpha is simply the persistent mycelium of Agaricus melleus, which grows on We have no doubt that another form or rotten stumps. variety of Rhizomorpha is the mycelium, or vegetative condition of Polyporus squamosus, and others, with more or less certainty, are referred to other species of Agaric and Polyporus. Something of the nature of Rhizomorpha is found amongst dead leaves, mostly in long, simple, rigid black threads, which in size and appearance are not unlike horse hair. These are believed to be the mycelium-or rather, we should say, the permanent mycelium, to distinguish it from the filamentous white mycelium-of some species of Marasmius. In tropical and sub-tropical regions these horse-hair filaments are very common amongst dead leaves, and are known to be sterile conditions of several species of Marasmius.

There is another condition which the mycelium of some Fungi assume that is something of a resting stage, and in former days these were classed under a genus called *Sclerotium*. They are in the form of hard, compact, irregular nodules, from the size of a pin's head to that of a child's head, according to the species. They are mostly dark coloured externally, and nearly white and horny within, with a firm cellular substance. We will commence with one that is well known, under the name of Ergot, and occurs on the spikes of rye, wheat, and



FIG. 2.—Ergot Sclerotia germinating. After Tulasne.

many grasses, converting the ovary into a *Sclerotium*, or replacing the ovary with a Fungus growth, whichever view pleases best. These abnormal growths are three times as long as the ordinary seed of the rye or grass, elongated, and a little curved, so that they look like a horn or spur projecting from the ear of grain. If a thin slice of the substance is placed

under the microscope, it will be seen to consist of a densely compact mass of cells, somewhat irregular from mutual pressure, with thick walls and rather oily contents. At last they are liable to become dissociated from the spike, and fall to the ground, where they will lie quiescent and unchanged through the winter. When spring arrives, active vitality recommences, and the sclerotium germinates by producing one, two, or more—generally several —little slender twisted stems, with a globose head, reminding one of a pin. The stem is whitish, and the head of a pale purple. It is within the globose head that the fructification is produced. This latter is the mature Fungus of the Ergot sclerotium, and is then called *Claviceps purpurea*, one of the Sphaeriacei (Fig. 2).

By way of illustration, we have indicated briefly the history and development of the Ergot sclerotium, but it will scarcely be consistent with the design of this chapter to repeat the process for other species. Another example may be found inhabiting the dead haulms of potato. First of all the haulms

MYCELIUM

are covered with a dense felted mass of white mycelium. When this is fully developed, scores and hundreds of little black points appear in the midst of the hyphae, averaging in size from a grain of sand to that of a small bean. These become indurated and hard, and, in fact, properly-constituted sclerotia, internally composed of polygonal cells. These also

subside into a condition of rest, in which they spend the winter, and germinate in spring. The resulting Fungus in this instance consists of similar slender twisted stems, but the head, instead of being globose, is cup-shaped, then flattened, bearthe name ing of Sclerotinia Libertiana. or,asknown in former years, a species of comycetes (Fig. 3).



Peziza, one of the Dis-FIG. 3.—Sclerotia germinating and producing Pezizae, A to D. Ascus and sporidia, E. Gard. Chron.

Several other instances might be quoted in which the Sclerotium, when germinating, produced a species of Peziza, especially a large one common in company with the roots of the Wood Anemone. A large species of Russula, common in the woods, turns quite black when dead and decaying. On the gills of these decaying Russulae many sclerotiae will be seen, resembling in form small grains of barley. These germinate speedily, and produce a little Agaric (Collybia tuberosa). In Australia a sclerotium nearly as large as the fist develops a tough gill-bearing Fungus, shaped like a wine-glass, named Lentinus cyathus. But a still larger sclerotium, which has been known for years as "Native Bread," and grows as large as a child's head, has been recently found to develop a white Polyporus with a central stem, and has been named Polyporus Mylittae.¹

¹ Grevillea, Dec. 1892, p. 37.

We have briefly directed attention to the ordinary developments of mycelium, whether filamentous or sclerotioid, but there are still one or two special modifications which must obtain a passing reference. Of these the mycelium of the Uredineae is deserving of mention, being formed within the tissues of living plants, and often starting centrifugally from a definite point of infection. The hyphae resemble ordinary mycelial filaments, but, like all internal mycelia, are delicate, branching and anastomosing so as to form compact cushions or spore beds, or, in other cases, much diffused and scattered. In annuals or upon deciduous parts the mycelium is, of course, only annual, but if it passes into perennial parts, as it may readily do in shrubs and other perennials, the mycelium becomes Take, for instance, the Juniper, in which the perennial. Gymnosporangium may be sought for and expected regularly year after year. In such species as have a scattered mycelium there is not much difference between the mycelium of these and that of other endophytes, but when the mycelium is circumscribed, the tissues are hypertrophied, and starch seems to be accumulated in the deranged cells. Leaves thus attacked never repair the injury, and the diseased spots are the first to die, and occasionally drop out, as we have seen with the large clusters of perfect-spored pustules in Puccinia deanthi. The mycelium of the Peronosporeae is more diffused than that of the Uredines, commonly penetrating the whole plant, descending into the stem and roots, and in the stems producing oospores, as the result of a sexual conjugation. In the Ustilagineae the mycelium is much more diffused than is usual in the Uredines, permeating the entire plant, and in perennial hosts producing fruit regularly year after year.

The *Phycomycetes*, which include those mould-like Fungi which bear inflated sacs at the apices of their fertile branches containing numerous spores (*Mucors*), have a mycelium without septae. The Mucors themselves are mostly saprophytes, and some of them have a profuse mycelium. The reproduction is both asexual and sexual, the sexual being developed from the mycelium; hence the mycelium in these Fungi, although at first only vegetative, becomes finally reproductive, and thus assumes a higher function. The process is after this kind: two short

MYCELIUM

branches of the mycelium approach each other until they touch at their apices. The branches swell and become club-shaped, including a rich store of protoplasm. At length the upper portion of each club is cut off by a transverse septum, and the two apical segments are fused into a globose body, the walls at the point of contact being dissolved. Thus we have two thick supporters, with a globose body suspended between them, which is to become the zygospore, resulting from the conjugation and coalition of the club-shaped branches (Fig. 4). The succeeding steps need not be detailed; the zygospore acquires a thick outer coat, and then becomes a resting spore, which only germinates after a period of rest. The same mycelium therefore produces



FIG. 4.-Zygospore of Mucor in course of formation. After De Bary.

erect carpophores, or conidiophores, surmounted by an inflated vesicle containing conidia, an asexual generation, and also pairs of nearly sessile branches, which collide and form a zygospore between them, a sexual generation. Similarly, in other families the two kinds of reproduction are developed, asexual and sexual, from different parts of the same mycelium, but not precisely in the same way, yet the details do not affect the mycelium greatly, except in the family to be presently alluded to.

The *Entomophthoraceae*¹ are those Fungi which are parasitic and destructive to insects, including the ordinary fly mould,

¹ The Entomophthoreae of the United States, by Roland Thaxter, 1888, Boston, U.S.

Empusa muscae. When the spore of one of these moulds alights upon the body of its favourite host-insect it sends out a germ tube, which enters the body at any favourable spot, and when this is once accomplished, it develops rapidly, at the expense of the tissues it replaces. It does not form a branched mycelium,



FIG. 5.-Hyphal bodies in Entomophthoraceae. After Thaxter.

but grows by the production of hyphal bodies (Fig. 5), which are short, thick bodies of variable size and shape, and these continue to multiply, by budding or gemmation, until they fill the insect. It is possible that in some cases a mycelium of the ordinary kind may be produced. When the whole interior is absorbed,

and of course the insect is dead, the vegetative stage ends, and the reproductive begins, by the protrusion into the atmosphere of conidiophores terminated by conidia, either singly or in bundles, until the body is covered with the conidia, ready to be dispersed. This is the asexual reproduction of conidia, but resting spores are also formed, which may be sexual or asexual,

according to the species. In some cases the conjugation of two threads of the mycelium, and in others the conjugation of two of the hyphal bodies (Fig. 6), results in the formation of a zygospore. There is a peculiarity about the conidia which may be noticed, which is, that should a ripe conidium not be able to find or enter a host-insect, it can proceed to germinate and form a secondary conidium, which has the same power of infection, and may be more fortunate. If this also fails, the secondary conidium may pro- FIG. 6.-Hyphal bodies in duce a third, so that the vigour of the

conidia is kept preserved until able to



Entomophthoraceae conjugating. After Thaxter.

Possibly the Isaria moulds, in the interior of infect a host. insects, extend their mycelium in a similar manner by budding, as they are also granular rather than filamentous.

In opposition to the views of some mycologists of experience and repute, we still remain persistent in our adhesion

MYCELIUM

to the vegetable nature of the Myxomycetes, and consequently regard the vegetative condition as upon an equality in function, if not in structure, with the mycelium. This was clearly the view of M. Léveillé, who termed it "a malacoid or pulpous mycelium." We see no objection to its being called a plasmodium-the name does not alter its character or functions. De Bary was content to admit that the wall of plasmodia, as well as the cell-walls of spores and other parts, gave a distinct cellulose reaction, and possibly cellulose in some form is general in Myxomycetes. And further, according to the same eminent authority, the presence of cellulose is the only character showing that these organisms are in touch with the vegetable This question we are not anxious to discuss further kingdom. here. Swarm-cells with the power of movement are produced on germination from the spores of Myxomycetes; these swarmcells ultimately coalesce and form a plasmodium, which is capable of passing into a resting stage, and sometimes to become surrounded by a colourless membrane. There are no threads or filaments, as in a filamentous mycelium, neither in the sclerotioid mycelium is there a similar resemblance; in fact, there is no greater difference between a plasmodium and a sclerotioid mycelium than there is between a sclerotioid and a filamentous mycelium. From the plasmodium are differentiated the carpophores, the receptacles, and the fructification of a Fungus, even although the plasmodium or analogue of mycelium is not filamentous, but rather resembles a sclerotium in a soft and pulpy condition.

Theoretically, mycelium originates with the germ-tubes which are protruded by spores or conidia upon their germination. It is easy enough to observe the process thus far, produced artificially by placing the spores in a nutritive fluid, but in the case of the larger Fungi the operation cannot be carried much further under ordinary circumstances. In the case of Agarics it is concluded that the mycelium produced by a number of spores unite in the production of a single Agaric, so that one specimen is the produce of several germinating spores. We know that the soil contains a great mass of mycelium in places where Fungi are found growing. Worthington Smith says¹ that the Agarics of the autumn spring up

¹ Reproduction in Coprinus, Grevillea, iv. (1876), p. 53.
from the mycelium formed during the fall of the previous year, and this mycelium has rested in the ground for twelve months. In digging up old pasture ground, or the dead leaves of an autumn which has passed, mycelium in a resting state is invariably found. We can hardly conceive of the preservation of the spores of an Agaric through the winter and an entire year, until the succeeding autumn, in any other way than by the production of a hibernating mycelium. The spores themselves have too delicate an epispore to resist the effects of cold. and we know from analogy that the resting spores of Algae and Fungi, when known to be such, are provided with a special thick outer envelope. The spores of Agarics are not thick coated, and are incapable of hibernation; hence we are driven to the alternative of a perennial mycelium. A theory was once propounded that a conjugation takes place in the threads of mycelium which results in the production of a fertile Agaric, the whole of whose fructification is thereafter rendered fertile, but this view has never been accepted. Notwithstanding all the theories, we are still in search of the process of fecundation in Hymenomycetal Fungi. All that we can contend for is the persistency of the mycelium as the means whereby the Mushroom Fungi are carried through the winter and reproduced in the succeeding year.

There is a prevalent opinion, in Germany at least, that "root fungi" are not always injurious to trees, but sometimes, on the contrary, beneficial. Frank¹ states that certain trees are unable to derive nutriment direct from the soil, but do this by means of a mass of Fungus hyphae which entirely invests the root, to which he gives the name of Mycorhiza. It makes its appearance first on young seedlings, and is replaced by fresh formations on older roots. He found it on the roots of every tree examined belonging to the Cupuliferae, and occasionally on willows and conifers, but considers it may only be formed in soils which contain a large amount of humus, or undecomposed vegetable remains. Through the Mycorhiza the tree absorbs not only water and mineral constituents, but organic substances derived from the humus. Two or three other authors have since confirmed this in ¹ Journ. Roy. Micr. Soc., vol. v. (1885), p. 844; vol. vi. (1886), pp. 113, 663.

the most important particulars, but not as to its constant presence.

The mycelium is the active agent by which Fungi disintegrate decaying organic matter, or prey upon and destroy the living, and so far as they derive nourishment from the substratum, their nutrition resembles that of flowering plants, but beyond this the mycelium is active in decomposing the organic matrix, the product of which is not required or taken up by the Fungus. Hence there are forms which are satisfied with taking up from living or dead substrata only so much as is needed for the construction of their bodies, as well as those which in addition produce copious decompositions in the substratum and destroy it. We may assume that the mycelium exerts a ferment action upon the matrix, although the quantity of the ferment may be small, and that these ferment actions first take place in order to convert a portion of the substratum into a form which is capable of nourishing the Fungus.

In the headings of the several chapters we have used terms in their general sense, representing the *mycelium* as equivalent to the vegetative system, the *carpophore* as the supporter of the fructification, or intermediary between the vegetative and reproductive systems, whilst *receptacle* is employed in a sense different from that which it holds in other branches of botanical science, and should be accepted literally as representing the envelope of the fructification, whatever its form may be, when any envelope is present. This definition is necessary so as to prevent confusion of the terms we have employed in a general sense, with their special application elsewhere.

CHAPTER III

THE CARPOPHORE 1

THE mycelium, in all its forms and variations, is but the prelude and preparation for the development of such parts or organs as may be necessary for the subsequent processes of The production of the carpophore is, in itself, reproduction. only a continuation of the process of vegetation, but that vegetation is no longer subterranean, subcuticular, or creeping; invariably it is more or less, in development, at right angles to the mycelium, and may be accomplished by the production of



Rhopalomyces.

special erect branches, or a stem compounded of an indefinite number of erect threads, agglutinated and consolidated together; whether it is to be the conidiophore of a mould, the stroma of a Cordyceps, the club of a Geoglossum, or the stalk of an Agaric or Boletus, it is the fruit-bearer, or carpophore, which is destined to bear the fructification of FIG. 7.—Unbranched the species. It may be reduced to its lowest carpophore of terms, and be practically obsolete, so that the receptacle is sessile, or nearly sessile, upon

the mycelium; still there is normally and technically a carpophore, which supports the organs of reproduction.

In the larger moulds generally the ascending hyphae are branches of the mycelium, and do not alter much in character except in being rather thicker and with more rigid walls, so as to maintain an erect position. These erect threads are in most cases clustered together, and are modified in ramification

¹ The term "carpophore," in its special sense, is usually restricted to forms of a distinct fruit, consisting of an aggregate of reproductive organs.

THE CARPOPHORE

according to the different genera. In certain cases, as in *Aspergillus* and *Rhopalomyces*, they are simple and unbranched up to the top (Fig. 7), but in the larger number of genera they are branched in the upper portion. Very often a great

number of these carpophores are produced in a large woollylooking patch, not rarely for an inch or two in length. Endogenous moulds, which produce mycelium in the interior of the tissues, send up little tufts of carpophores through the stomata, and these grow in patches. Well-known examples are to be found in the genus Peronospora, such as



FIG. 8.—Branched carpophore of Peronospora.

the mould on parsnips and onions (Fig. 8). In the genus *Ramularia* the mycelium is internal, and the conidiophores pass in the same manner out into the atmosphere; but they are usually short, often unbranched, with a single conidium. In *Oidium* the mycelium is external, and the erect hyphae are simple, but it is only the short lower portion which is truly a carpophore, for the upper portion is constricted successively, and the joints fall off as they are formed, and become conidia.

There are also genera in which the carpophore is compound —that is to say, a number of threads are combined so as to form a common stem, which is consequently thicker and more permanent. Either these individual hyphae diverge at the apex, or they remain united and form a capitulum, as in *Stilbum*. When the combined threads form only a short erumpent stroma, as in *Tubercularia* (Fig. 9), the carpophore is reduced nearly to its lowest denomination, and is scarcely more than an erumpent pustule. All the foregoing forms are repeated in

the Dematioei, or black moulds, the chief difference being in the dark-coloured, more rigid, and carbonised hyphae.

Resembling the moulds in external habit, the Mucors resemble them also in the carpophore, which is sometimes forked two or three times, but not dendritically branched. In Pilobolus the carpophore is curiously inflated, like a bladder (Fig. 10).

We have in remembrance a pseudo-analogy which some



FIG. 9.—Compound carpophore of Tubercularia.

few years since became current-that the type of organisation in a Mucedinous mould was repeated, with modifications, in the structure of Agarics. The mycelium, it was contended, was common to both. From the mycelium arose the carpophore, which was a compound stalk, in which a myriad of erect hyphae were combined; in the pileus the combination was continued of the branches, and then down to the basidia, which were the terminals of the branchlets, with the spores, or conidia on spicules, as in such a genus as Rhinotrichum.

This was a fanciful representation, since the analogy, even if it held good elsewhere, was broken at the hymenium, and the basidia were therefore not in continuity with the trama. In the Hymenomycetes, or at least in the Agaricini, the stem is continued from the mycelium at right angles, as in the moulds, and is compounded of an infinity of elongated parallel cells; these are sometimes deficient in the centre, and the carpophore, or stem, becomes hollow. Leaving the appendages to the stem out of question, it is still an erect carpophore, and hence its functions are the same-that of elevating the re- FIG. 10.-Inflatproductive organs into the atmosphere. In the same manner also the materials of nutrition,



ed carpophore of Pilobolus.

derived by the mycelium from the soil, are conveyed upwards to the residue of the plant. The veil, where it exists, is a supplementary appendage, not found in the moulds, and is

THE CARPOPHORE

simply an extension of the margin of the receptacle, or pileus, for the projection of the young hymenium. In *Boletus* and the stipitate *Polyporei*, *Hydnei*, etc., the carpophore is of the same type. In such of the species of *Pleurotus*, *Fomes*, etc., as have no stem the pileus, or receptacle, is sessile, and the carpophore is reduced to a mere disc, or is obsolete.

The external surface of the stipe or stem is sometimes glutinous, as in the section Myxacium of the genus Cortinarius ; or it is velvety, as in such species as Collybia longipes and C. velutipes; or it may be woolly, chiefly at the base, or broken up into scales; and all these conditions doubtless serve in some way to fulfil some purpose. Worthington Smith has suggested that they are probably of service to arrest the spores as they fall from the hymenium, and, as he thinks, also the deciduous cystidia. Of the internal structure M. de Seynes remarks that the collective cells, which form the stipe, and afterwards expand into the cap, are generally rather uniform, long, fibrous, often much separated, rarely ramified, presenting at times in their distance from each other, at others in their dimensions, differences which, on the fissure of the stipe, present an aspect either fibrous, granulated, spongy, or woolly. The cellular fibres are always closer and more compact at the cortical part. Those peculiar lactiferous vessels which convey the milk, so conspicuous in Lactarius, are not confined to the cap, but are present also in the stem, although possibly not quite so abundant, but they must be very numerous in the stems of one section of the genus Mycena where the milk is almost confined to the stem. In Mycena leucogalus it is quite white, in Mycena haematopus, of a blood red; in Mycena crocatus it is saffron yellow, and in Mycena galopus it is described as white, but it is often watery, or with a tinge of white, like milk and The quantity of milk depends much on the dampness water. of the habitat.

In such degraded forms as *Corticium*, *Radulum*, etc., the carpophore is obsolete, and the receptacle is reduced to a fibrous stratum, which is seated directly upon the mycelium, and only the hymenium receives its proper development. Other genera require little observation, since in some forms of *Thelephora*, in *Lachnocladium*, and in *Clavaria* and its allies,

we have the closest resemblance to the carpophores of the moulds, even to dendritic branching, but of a larger and more robust habit. Isaria is often closely imitated in external appearance by Clavaria. The most anomalous of all groups in respect to the carpophore is the Tremellini, but even in this there is a link in Guepinia, Gyrocephalus, and Ditiola. We have not forgotten that in some of the Basidiomycetes the whole of the Fungus, in its earliest stage, when seated upon the mycelium, and before the development of the carpophore, is enveloped in a volva. This is not, however, more than a generic distinction, in any case, and reaches its highest development in Amanita, Volvaria, Ithyphallus, Clathrus, etc. It might be compared to the calyptra in mosses and liverworts, but is by no means so general, and without so much significance.

The Gastromycetes are not so well provided with a carpo-



FIG. 11.—Carpophore in *Ithyphallus impudicus*.

phore as the Hymenomycetes, but at the same time there is no degradation to resupinate or overturned forms. The majority of the Phalloid Gastromycetes have a distinct carpophore, which is functionally the same as in Agarics, but the structure is more loosely cellular (Fig. 11), and, from rapidity of growth, lacunose. It is only in Fungi like these, which are quick to decay, that we encounter such a loose texture of cells in the carpophore. In Podaxis the form of the entire plant resembles that of Coprinus, but the carpophore is rigid, almost woody, as it is also in Batarrea, Xylopodium, and Tylostoma. The carpophore in Secotium approaches the type of the coriaceous Agaricini, such as Lentinus. There are no other genera which call for special notice respecting the carpophore, which is short, and almost spurious in Scleroderma and

Polysaccum, rare in Lycoperdon, and then only a prolongation of the spongy base of the receptacle. In nearly every genus except Gyrophragmium, Podaxis, and Secotium, it expands into, and is confluent with the receptacle. The subterranean species, like the truffles, have no carpophore.

It is not difficult to comprehend the functions of the

THE CARPOPHORE

carpophore in the Hymenomycetes, in all of which the hymenium is inferior, and therefore it is essential to its development that the receptacle should be raised sufficiently above the matrix to permit of a free development of the hymenium. The carpophore is only suppressed or obsolete when the receptacle grows out at right angles to the matrix, and then no stem is essential. Furthermore, so many species grow on vegetable debris and dead leaves, hence a stem is necessary to push the All collectors know how much the pileus into the light. stems are lengthened beyond their normal proportions when the mycelium is deeply imbedded in the loose soil, and that the hymenium is not developed until the pileus is elevated into the light. In the Gastromycetes the hymenium is not inferior, so that it is sufficient if the receptacle is just above the soil, and hence the carpophore is short. The Phalloidei are exceptional, as the hymenium is not concealed, but must be well exposed, in order to mature speedily.

All the remainder of the large fleshy Fungi belong to the *Discomycetes*, in which the hymenium is exposed on the upper surface, and therefore, as might be expected, the carpophore is

often short or absent. The Morels and *Helvellas* are all stipitate, and the receptacle is like a cap or hood; but as they are terrestrial, often growing in loose soil and amongst debris, a carpophore long enough to bring the receptacle into the light is essential. In this case the substance scarcely differs from that of the cap, but it is robust, and the external stratum is not cartilaginous. In several genera of terrestrial habit the form is clavate, with a carpophore long enough to bring the



FIG. 12.—Receptacle or cup of *Peziza*.

hymenium through the short grass into the light, just as in simple club-shaped forms of *Clavaria*. We need only to allude to the old genus *Peziza*, whatever the modern designation may be, for all of the species are cup-shaped in form (Fig. 12), and the hymenium is turned to the light, hence all the carpophore which is necessary is that which is sufficient for such a purpose,

so that usually the carpophore is short, and often reduced to a mere point. Species such as that which grows on the sclerotium of anemone roots are variable in the length of the carpophore in proportion to the depth at which the sclerotium is buried, or of such as grow on acorns or beech-mast lying on the ground the carpophore is long enough to bring the hymenium to the light. *Peziza aurantia* or *Peziza badia*, growing on naked soil, are fully exposed, and hence are sessile. Wherever, from its matrix or peculiar habit of growth, a species, if sessile, could not expose its hymenium to the light under ordinary circumstances, a carpophore is usually present. Species which grow beneath the bark of branches, and break through, have invariably a short carpophore to raise the disc to the surface.

Some special forms of carpophore are to be found in the *Pyrenomycetes*, where the fructification is capsular, and the receptacle small and simple. In this case the carpophore is not, except rarely, that of a single individual, but of a colony



FIG. 13.—Isaria farinosa on pupa of moth.

or an agglomeration of individuals, each individual being represented by the fruit receptacle, the carpophore being a vegetative branch, developed from the mycelium, specialised to carry the fructification, as the conidiophore of a mould is specialised to carry a great number of conidia. For example, the pupa of a moth becomes filled with mycelium, which, in the first instance, developed conidia under the form of *Isaria farinosa* (Fig. 13); finally, a club-shaped fleshy protuberance called a stroma grows from the surface of the pupa in connection with and continuation of the internal

mycelium. This fleshy stroma is at first only a sterile branch from the mycelium, like the stem of an Agaric, but ultimately the whole of its upper surface is covered with an indefinite number of minute receptacles, which are developed in a colony at the apex of a carpophore. The insects, whether larvae or pupae, on which these Fungi are developed are at the time buried in the soil, and the function of the carpophore is to carry the fructification into the light, so that sometimes it has to be prolonged several inches before

THE CARPOPHORE

the fructifying surface is sufficiently raised above the soil to attain its development (Fig. 14). The carpophores vary not only

in length for the same species, according to circumstances, but also in form, according to the species. In some it is simple, and in others branched, but the receptacles are always densely accumulated about the apices in this genus of Hence we recognise again that a Cordyceps. carpophore is a contrivance which is resorted to in order to bring the fructification into the air and light, and is lengthened or shortened in conformity with that object. In the genus Xylaria the form of carpophore is similar, but its texture The colour is normally black exterdifferent. nally, white and corky within, and it is wholly tough and hard. The species grow on putrid FIG. 14.-Clavwood and rotting leaves. In an allied genus, Thamnomyces, the carpophore is very long and



ate stroma of Cordyceps.

thin, often like horse hair, running amongst dead leaves and vegetable debris.

It is notable how some of the simplest forms of carpophore are repeated in different groups of Fungi far removed from



FIG. 15.-Globose stroma of Hypoxylon.

each other in structure. This is the case where the whole Fungus is clubshaped, as it is in Clavaria pistillaris, and again, even as to colour, in Xylaria involuta. Others of a smaller size, but of a like form, will be found in Clavaria ligula, Leptoglossum olivaceum ; Xylaria rhopaloides ; Geoglossum hirsutum, and Hypocrea ophioglossoides.

No one can doubt, after tracing the gradations of form in Xylaria, that the spherical carpophores, not only in

Xylaria, but also in Daldinia, Glaziella, Sarcoxylon, and the Sphaeroxylon section of Hypoxylon, are of the same character, and have a similar purpose to the foregoing (Fig. 15). Possibly the globose forms may primarily serve to expose the largest surface of immersed receptacles to the light, rather than elevate

them from darkness into light, as was seen to be the first function of the long-stemmed carpophores. Everything indicates in the Pyrenomycetes that there is some necessity for exposing the fructifying surface to the light; whether on carpophores or effused in a stroma, only one stratum of perithecia is the rule, a double series the very rare exception.

CHAPTER IV

THE RECEPTACLE

HAVING described the mycelium, already designated as the vegetative Fungus, and which is always present, we passed to an outgrowth of the mycelium (sometimes suppressed), which, as the carpophore, is destined to support the receptacle. It is the latter which contains the fructification, or, in the case of naked fruits, supports the fructification itself. It may be urged that the receptacle is part and parcel of the fructification, but it is really no more intimately so than are the receptacle or the calyx and corolla in flowering plants. This, however, need not be discussed, as it is only a question of analogies. What we desire to include under the present designation is the development, or modification, of the superior continuation of the carpophore, which encloses or supports the essentials of fructification. In the absence of any distinct or evident carpophore, it is still the immediate supporter or envelope of the fructification, which in that case is sessile upon the mycelium.

This receptacle may be variable in form, and be known under different designations, but its function is the same that of supporting or enclosing the hymenium, wherever a hymenium or its analogue is present. This organ will be represented in some cases by a pileus, in others by a peridium, an excipulum, a perithecium, a sporangium, or even a proliferous stratum.

The best-known form, because the largest and most conspicuous, is the *pileus*, which is characteristic of the *Hymenomycetes*. It forms the cap in Agarics and the pileus in *Fomes*, *Polystictus*, etc. This cap in Agarics and allied genera

surmounts the stem or carpophore, and bears on its under surface the hymenium or fructiferous surface. It follows the same type in the Agaricini, Boleti, some Polyporei, and Hydnei. This type is a convex, or primarily convex, orbicular expansion of the apex of the stem, with a more or less distinct pellicle on its upper surface, an intermediate stratum, and its lower surface covered by the hymenium. In this type, then, it is a hymenophore, as it is in other forms of Hymenomycetes. This cap (Fig. 16) not only surmounts, but it is continuous with the stem, and for the most part conforms to it in texture. In some cases it passes down in plates on the under surface between



FIG. 16.—Agaric. A, young; B, mature; C, section; p, pileus; s, stipe; v, volva; g, lamellae or gills; a, annulus or ring.

the folds of the membrane which bears the hymenium, and is the trama. The superior cuticle or pellicle is sometimes so distinct from the subjacent stratum that it may be stripped off, but in other species it is so intimately incorporated with the substratum that it is inseparable. From the margin of the cap this cuticle is sometimes extended inwards and united to the stem, covering the young hymenium, and forming a veil. Externally the cuticle may be quite dry or viscid, or even covered with a slimy gluten, as in *Agaricus mucidus* and *Agaricus aeruginosus*. In some cases the cuticle is compara-

THE RECEPTACLE

tively thick, and consists of an outer and inner layer, the former breaking up as the cap expands, and adhering in patches or scales, as in Agaricus procerus, whilst the inner silky, fibrous layer is closely adnate to the flesh. Not uncommonly the cuticle, without breaking up, is finely striate with innate silky fibrils, or shining with a satiny lustre. The flesh beneath the cuticle differs somewhat in different species, in texture and in comparative thickness, but is always thinnest about the margin, sometimes scarcely exceeding that of the cuticle. The cells of the fleshy substance of the pileus in Agarics are more branched than those of the stipe. They will form, by anastomosing and crossing each other, a sort of polygonal trellis-work, and in the meshes so formed there is a second system of larger cells. Corda alludes to them, especially in the Russulae, and he says, "These two forms are not always neatly separated, but pass, as the organ requires, more or less rapidly, one into the other, or, what is more rare, they are substituted the one for the other. These two forms of tissue take part, generally both together, in the structure of the hymenium, each giving birth, or both together, to one or many organs of the hymenium." 1

The lactiferous tubes in such a genus as Lactarius are often of larger dimensions than the ordinary tissue, and M. de Seynes protests against their being called "vessels," because, if the cells are very long, yet it is possible to see that they are divided transversely. In Fistulina, which contains an abundant red juice but more fluid, it is contained in special varicose and sinuous tubes, like the laticifers, but furnished with transverse divisions. On approaching the gills the same series of cells are curved and recurved, showing that the milky secretion is there more abundant. As to the functions or import of this juice, that is still an obscure point, for there are so very many Agarics which do not possess it at all, or if present, it is in smaller quantity, and not equally visible. It is well enough known that in Lactarius the milky juice descends into the hymenium, for if the gills are cut or bruised, it oozes out, and hangs suspended in drops. When dried it is readily seen to be resinous.

¹ Corda, Icones Fungorum.

33

34

No one has yet paid much attention to the coloration of the pileus in Agaricini, which is subject to much variation, due in part to external circumstances, as was pointed out by M. de Seynes. Albinism is one of the variations which he observed in well-recognised species. It occurs in Hygrophorus calyptraeformis, Amanitopsis vaginata, Russula fragilis, and some others. "By the side of this fact there is another quite opposite, the greater intensity of coloration, according to the temperature." For instance, he found during the winter Tricholoma nuda, according as the temperature falls, of a dark violet, almost black, or a deep brown. When spring arrives it is found almost white, shaded with lilac or fawn colour. Tricholoma terreus and Collybia dryophilus will present the same phenomena. He found also, in a cold December, Volvaria media of which the pileus was almost black; ordinarily it is nearly white. Upon microscopical examination he found that there was no new production of cellular elements, but simply a greater agglomeration of pigmentary granules. He also indicates that he has often been struck with the deep coloration of Armillaria mellea and Hypholoma sublateritius, which were seen by hundreds during a low temperature $(41^{\circ} \text{ to } 42^{\circ})$ Fahr.), the aspect of which differed very much from the same species found in the woods during the fine days of autumn.¹ The same writer adds that, from numerous observations, he is certain that, although the cold has an influence upon the intensity of coloration amongst Agarics, it does not follow that in the middle of winter specimens may not be found of the normal colour, either by being shaded, or in proximity to heat. The effects of external circumstances on the variation of the fleshy Fungi deserves more serious attention.

In some few instances the fleshy stratum is almost obsolete over the entire cap, as in *Hiatula*, some species of *Coprinus*, *Bolbitius*, etc., and in some exotic species of *Marasmius*. In such cases the cap is so thin—like a membrane—that when moist the gills may be seen through the substance. In *Boletus* the cuticle is sometimes distinctly velvety, and the flesh is comparatively thicker than in Agarics. In *Polyporus*, *Fomes*, *Polystictus*, *Hydnum*, etc., the entire substance is more

¹ Grevillea, vol. ii. p. 12.

THE RECEPTACLE

woody, contains less moisture, and consequently dries with but little shrinking or change of form.

As the carpophore is sometimes obsolete in the Hymenomycetes, so also is the receptacle or pileus reduced to a simple stratum, which intervenes between the mycelium and the spore-bearing surface. These are undoubtedly rudimentary forms, but they are very numerous, sometimes constituting entire genera, as in Poria, Coniophora, Corticium, etc., besides numerous species in other genera. For the most part a thin fibrous stratum, differentiated from the fibres of the mycelium, forms, and supports the hymenium. Possibly the old genus Ozonium consists entirely of these suppressed pilei, which never form a hymenium. The supporting stratum is very peculiar in Asterostroma, where the hyphae are stellate, and in Thelephora pedicellata they assume a dendritic form. It is not uncommon to find specimens of Corticium in which the hymenium is only in patches, or, in some cases, never formed at all, so that the whole Fungus remains in the vegetative stage, that is to say, mycelium, and a sterile fibrous stratum to represent suppressed carpophore and atrophied receptacle.

The second type is deficient in any appreciable carpophore

or stem, and consists of a pileus of a semicircular outline, attached at its base to the matrix and its own mycelium (Fig. 17). In these also there is a superior stratum, which may be thicker than in the preceding, an intermediate substance, and an inferior hymenium. The upper



FIG. 17.-Fistulina hepatica, sessile pileus.

stratum in *Polyporus* and *Fistulina* is hardly distinct from the intermediate; but in *Fomes* it usually forms a firm hard crust, very hard and horny in *Fomes australis* and

Fomes cornu-bovis, but smooth, and mostly shining, often laccate, as if varnished. According to Wettstein,1 this is due to the secretion of resin which oozes from peculiar hyphae and flows over the surface of the pileus. The exterior of the pileus exhibits deep concentrated channels, which mark the annual additions at the circumference. The substance is often very thick and fibrous, the fibres radiating in every direction from the base. They may continue growing by the addition of external zones for many years, always the oldest posteriorly. From these Polystictus differs in being much thinner, and the cuticle is fibrous, hairy, woolly, or strigose, and concentrically The substance is dry, tough, and leathery, usually zoned. flexible. In so far as these features are concerned, Stereum not only resembles Polystictus in appearance, but also in texture, and so does Hymenochaete ; whilst Hexagona differs more in the hymenium than in anything else. These, therefore, may be accepted as representing the two forms of the sessile receptacle in Hymenomycetal Fungi-the woody by Fomes, to which might be added Daedalea, and the coriaceous by Polystictus, and the others above named.

The next form of receptacle to be adduced is the peridium, which completely encloses the reproductive organs, and may also be supported on a distinct carpophore, or it may be sessile on the mycelium, or invested by it, as in some subterranean species. The Gastromycetes furnish this kind of receptacle,



and section.

which is very often double, typically globose, the outer coat or exoperidium being a continuation of the cortex of the carpophore when the latter exists. The internal cavity is filled with the reproductive bodies, which are only liberated by the rupture of the coat of the peridium. The inner FIG. 18.-Lycoperdon, peridium coat or endoperidium is often thin and membranaceous, and may either be

wholly separated from the outer or adnate therewith (Fig. 18). A prolongation from the carpophore sometimes protrudes into the central cavity in the form of a columella. The outer coat or

¹ Verhand. Zool. Bot. Gesell., Wien, xxxv. (1886), p. 29.

THE RECEPTACLE

exoperidium may be tough and leathery, and in Geaster it splits downwards from the apex into several triangular lobes. In Bovista it is fragile and evanescent. In Lycoperdon it breaks up into granules, warts, or spines, which adhere for some time to the inner and persistent peridium. In Polysaccum and Scleroderma the periderm is not differentiated into two coats, but in the latter the exterior cracks into warts or frustules. In this form the receptacle is an entirely closed envelope, in which the fructification is completely concealed until it is quite mature, and then it either opens with a small orifice or is irregularly ruptured. Hence the light is not essential to the perfection of the fruit, and the peridium might almost as well remain in the soil, which it has a tendency to do in some species of Scleroderma, and does completely in the Hypogaei. In the majority of species the substance of the peridium is tough and leathery, and so persistent that it often remains behind long after dehiscence and the dispersal of the spores.

A third form of receptacle is the excipulum or cup-shaped receptacle, which, although often closed when young, is soon

expanded so as to expose the disc or hymenium to the full light; in fact they are heliotropic, for they turn the disc as much as possible towards the sun. The type of this form is to be found in the old genus Peziza, now split up into many genera, but the form and structure of the excipulum is the same throughout (Fig. 19). The external stratum of cells does not form a separate cuticle, but is continuous with

the subjacent cells, and usually consists FIG. 19.-Receptacle of Peziza, of smaller or elongated cells, which



with section and ascus.

may be coloured, and either mixed with or prolonged into hairs, usually most strongly developed about the margin of the excipulum. Within the cuticular layer lie the subhymenial cells, on which rests the hymenium or fruit-bearing surface. The attributes of this form, therefore, are a cup-shaped receptacle, with the mouth turned to the light, and composed of an external and internal series of cells, the latter supporting

a compact hymenium. The substance of the cup and entire Fungus is most often soft and fleshy, and therefore they are more or less hygrometric, closing when dry and expanding Whether naked or clothed with hairs, the when moist. exterior is usually dull and sombre-coloured, so as scarcely to be distinguished from the matrix on which they grow. similarly-shaped receptacle is to be found in Cyphella amongst the Hymenomycetal Fungi, in Cyathus and Crucibulum amongst the Gastromycetes, and in Aecidium amongst the Uredines; besides partial resemblances amongst the Sphaeropsideae, and a few of the compact moulds, such as Volutella and Chaetostroma. The closing of the margins of the cups, and the long marginal hairs which in dry weather cover the hymenium, serve as a protection against evaporation, to which, from their fleshy substance and exposure, they are peculiarly liable. Some minute species, which are erumpent, retract themselves within shelter of the cuticle as they lose their moisture, and can only be distinguished with difficulty.

Another form of receptacle is represented by thousands of species, and that is the *perithecium*. This is a minute form,





FIG. 20.—Perithecium with section.

seldom exceeding a rape-seed in size, and usually very much less. It may be characterised as a globose flask with a very short neck, but this form is variously modified (Fig. 20). Sometimes it is seated directly upon

its mycelium, and sometimes sunk in a stroma which These receptacles may be superficial, arises from a mycelium. on the surface of the matrix, or either wholly or partially The globose form may be flattened at immersed. the base, and the neck be very much elongated, like a horn, or absent altogether; and they may grow singly or in company. In some genera the perithecium is soft and fleshy, and then pale or brightly coloured, as in Nectria. It may be thin and membranaceous, as in Sphaerella; or it may be coriaceous and tough, as in Botryosphaeria; or carbonaceous and brittle, as in Externally it may either be smooth and shining, Rosellinia. or mealy, or warted, or bristly, or woolly. The apex is always closed, except for a minute pore or ostiolum, and this is only

THE RECEPTACLE

absent in a few genera. In one group only, the Lophiostomaceae, the mouth is broad and compressed. The fructification therefore is always enclosed, as it is in the case of a peridium, but this is their only point of agreement. Whatever the form of the carpophore, the perithecia are always crowded together on the upper portion, and even when the carpophore is globose it is flattened at the base, and as the perithecia approach the base they are smaller, less numerous, and often imperfect. As already stated, the perithecia are always peripherical, and in a single series; but if, in rare cases, there is a second series, the necks of the perithecia are elongated so as to reach the surface of the stroma. When a great number of perithecia are collected together, and immersed in the matrix, a kind of stroma is formed from the matrix, as in Eutypa; but when on the surface, a regular stroma is formed upon the mycelium, which is fleshy in Hypocrea and carbonaceous in Hypoxylon, and the perithecia are closely packed and immersed in the stroma, which is per-

forated by the ostiola. The densely aggregated perithecia may sometimes be fused together so as to resemble an effused stroma. There are some genera in which the perithecia seem to be obsolete, or only formed from the stroma, in which the perithecia appear only as cells, as in *Phyllachora*; but the walls of the perithecia are possibly fused with the stroma and not wholly absent. The character of the fructification may be entirely different, while that of the perithecia remains the same. The same peri-



FIG. 21.—Receptacle of sporomega in *Hysteriaceae*, with ascus.

thecium, to all external appearances, may belong either to the *Pyrenomycetes* or the *Sphaeropsideae*. It may be a *Diplodia* or a *Plaeospora*.

It may be necessary to refer incidentally to a modification which is almost intermediate between an excipulum and a perithecium, which is prevalent in the comparatively small family, the *Hysteriaceae*. Here the excipulum closes from two opposite sides, leaving a slit down the centre. When well moistened

these excipuli expand so as to be nearly cup-shaped, and a compact disc is exposed (Fig. 21). This corresponds to the cups of the *Discomycetes*, but the substance is leathery or carbonaceous, and when closed the receptacles approach the *Lophiostomaceae*, which is sphaeriaceous. Nevertheless the most evident affinity is with an excipulum, in the broad expanding mouth and the definite disc, very evident in *Tryblidiella rufula*, and its relationship with the *Discomycetes* would be through *Phacidiacei*.

Other modifications need not be particularised, since these principal types will be sufficient to indicate the character of the receptacle in the majority of Fungi. We have the vegetative system represented in the mycelium, which sends up erect or compound branches in the form of a carpophore, for the support of the receptacle in all cases where the receptacle is stipitate, or, where the receptacle is wanting, then to support the naked fruit.

CHAPTER V

THE FRUCTIFICATION

THE contents of the various forms of receptacle already described, and those forms of fructification which are capable of being produced naked, without a receptacle, next demand attention. The best-known to the general public, and therefore the most interesting, are those large and conspicuous Fungi which pass under the name of Mushrooms or Agarics, and the woody Polypores, with the spore-bearing surface on the under side. In more scientific language, these are the Hymenomycetal Fungi, and so called because the hymenium or fructifying surface is naked, and produces naked spores. From what has preceded it will be remembered that a fleshy or woody pileus or receptacle, sometimes with, and sometimes without a stem, is the supporter of this kind of fructification. To the eye it presents the appearance of a continuous surface extending over plates or gills in the Agaricini, lining the interior of parallel tubes in the *Polyporei*, covering the outer surface of teeth or spines in the Hydnei, disposed over a nearly even plane in the Thelephorei, effused over an erect, simple, or branched carpophore, but without receptacle in the Clavariei, and immersed in a gelatinous stratum in the Tremellinei. Under all these modifications the primary elements of the hymenium are the same, or chiefly so; that is to say, there are one, two, or three kinds of elongated cells, packed side by side and called respectively basidia, cystidia, and sterile cells. Only the first kind are fertile, and bear at the apex four spores, surmounted on short slender spicules; the cystidia¹ are

¹ The usual interpretation of the function of cystidia is, that they are simply mechanical contrivances projecting from the surface of the hymenium, and thus keeping the gills or lamellae apart.

usually present, mixed with the basidia but rather larger, and the sterile cells are smaller and almost of the nature of, or analogous to, paraphyses (Fig. 22). De Seynes regards all three forms as modifications of the same organ, *i.e.* the



42

basidia, of which the spore-bearing are the fertile basidia, the cystidia are hypertrophied basidia, and the sterile cells atrophied basidia. All these cells are continuations and terminations of the tissues of the receptacle, sometimes with three or four subspherical cells intervening. The basidia are elongated clavate cells, or sporophores, filled with a granular fluid, surmounted by four short slender tubes, or spicules, each of which expands at the apex and becomes a spore; into which the contents of the basidium pass, leaving the basidium empty, so

that when its duties are completed it collapses and shrivels, then falls away. The spores thus formed by budding or gemmation, as far as known at present, are asexual and only gemmae. Many efforts have been made to prove them otherwise, but none of these have been confirmed. The spores themselves are unicellular (except in the Tremellini), and may be colourless or coloured. Modifications seem to take place in the cystidia, in different genera, independent of any difference in size. In the genus Peniophora they evidently become encrusted with lime and granular, so as to present quite a distinct appearance; in this condition they have been called "metuloids." In Hymenochaete and some species of Fomes the normal cystidia are replaced by rigid coloured setae, which may be modifications of cystidia. Corda regarded these peculiar cells as representatives of male organs, and called them antheridia; and a similar interpretation has been given to their functions by Worth-Most mycologists coincide in the opinion ington Smith. that a sexual apparatus has not yet been discovered in the

FIG. 22.—Basidia (b) and cystidia (c) of Agaricus; (a) paraphyses.

Hymenomycetes, and that it is scarcely probable that sexuality exists.

The contents of the closed receptacle of the second type enumerated in the preceding chapter—the peridium—differ in some features from the foregoing, although they accord in the spores being produced upon basidia. In this case there is no effused and exposed hymenium, but the interior of the peridium is occupied and filled with the gleba, or entire reproductive mass, which is at first homogeneous. Afterwards minute rifts are to be observed in the gleba, which increase in size, and ultimately form a labyrinth of cavities. The walls of these cavities are composed of hyphae, and the inner face is converted into a hymenium, the basidia of which are the

terminations of the hyphae of the walls. These basidia are more variable than in the Hymenomycetes, and the number of spores not so constant (Fig. 23): in the *Hymenogastreae* from one to four; in the *Phalloideae* from four to eight; in *Bovista* and *Lycoperdon* four and terminal; but in *Tulostoma* four and lateral.

Hence it will be observed that the spores are FIG. 23.—Basidium and spores of Lycoperdon. lining the walls; but the entire mass, or

gleba, is contained within a closed peridium, which is not ruptured until the spores are mature. When this takes place the entire gleba will be found in most cases (exclusive of the Phalloideae and the Nidulariacei) to be converted into a finely pulverulent mass, mixed with fine fibres. The powdery mass consists of the ripe spores, and the fine fibres are the remains of the internal hyphae, now called the capillitium. In the Hymenogastreae, which are the subterranean Gastromycetes, the walls of the cavities are more persistent, and therefore there is no capillitium, and the peridium is not ruptured when mature. One or two features of the spores are in contrast with those of the Hymenomycetes, that they are for the most part coloured, often warted, or spinulose, whereas the majority are also globose in form, except in the subterranean The basidia can be seen only whilst the gleba is species. young, for before the spores are mature they are dissolved away



43

The *Elaphomyceteae* correspond to the *Hymenogastreae* in being subterranean, similar in form, and alike enclosed within an indehiscent peridium; but they differ in the spores being enclosed within asci, instead of being produced on basidia, and in this respect are allied to the *Pyrenomycetes*.

In so far as their final, and reproductive, stage is concerned, the Myxomycetes resemble the Gastromycetes; they are sometimes stipitate, possess a distinct peridium, in which the spores are enclosed until maturity, and the latter are mostly coloured, globose, sometimes rough, mixed with the threads of a capillitium. On the other hand, the early or vegetative stage is so different, that the ancient notion of their affinity must be abandoned, although they are entitled to mention in this place as Fungi which produce their fructification enclosed within a peridium. Notwithstanding this, there are those who regard it as heresy to mention the *Myxomycetes* on the same page as the *Gastromycetes*.

The fructification, which is produced within an open cupshaped excipulum, is of more than one kind, but the most



FIG. 24.-Section of hymenium in Peziza.

important is that of the *Discomycetes*, in which the spores are ascomycetous — that is to say, they are produced within asci. In describing the receptacles it was stated that the fructiferous surface was a compact stratum or hymenium, which

overspread the interior of the expanded receptacle. In this instance the fruit-bearing surface is superior, and soon fully exposed to the light. It is plane or slightly convex when moist, depressed and concave when dry, from the contraction of the receptacle, and often brightly coloured (Fig. 24). The hymenium, or disc, is composed of elongated cylindrical or clavate cells, which are formed of a delicate hyaline membrane, splitting at the apex, or opening with an operculum. These cylindrical cells are closely packed side by side and constitute the asci,

THE FRUCTIFICATION

which are generally mixed with slender threads termed paraphyses, and these two bodies together compose the

hymenium. Each ascus when mature encloses eight, more rarely four, or sixteen, sporidia,¹ often globose or elliptical, and uncoloured. The paraphyses may or may not be abortive asci, the apex may be attenuated, or it may be thickened in various ways, and in the latter case often replete with a coloured protoplasm which imparts the colour to the disc. We are only desirous of explaining the normal form and structure, without regard to the minor differences which enter into the characters of the different genera. We may term the above the Pezizaeform type, which is represented by some two thousand species.

The question as to the nature and mode of derivation of the ascospores is at present scarcely more than problematical. No male organs have yet been found in consort with the thecae, and there is no reason to assume that ascospores are the result of sexual union. The only evidence is that offered of conjugation in the earliest stage of the receptacle, by means of which the entire cup and its contents FIG. is the sequence of a sexual act. De Bary, Woronin, and Tulasne are the observers on

with sporidia and paraphyses.

whom this phenomenon rests. It is to the effect that a

¹ It will be well to indicate here the names which are applied by the best authorities to the spore in its relation to the different families of Fungi. Although these names are somewhat arbitrary, the student will find them employed almost universally in systematic books.

Spore, without asci, in perfect Fungi, such as the Basidiomycetes.

Sporidium, enclosed in asci, in perfect Fungi, such as the Ascomycetes.

Sporule, without asci, in imperfect Fungi, enclosed in perithecia, such as the Sphaeropsideae.

Conidium, without asci, in imperfect Fungi without a perithecium, such as the moulds, or Hyphomycetes, and Melanconiaceae.

In Uredines and Phycomyceteae special modifications are employed which have reference to their development.

Spermatia, stylospores, and clinospores are merged in sporule.

25. - Ascus



specialised branch of the mycelium, which is thicker than the rest, is always to be found in close proximity to certain filaments, the short curved branches of which rest their extremities on the turgid branch first named, and which is termed the vermiform body or scolecite. At the point where these two organs meet there is a circular perforation, and one of the cells appears to transfer to the other a portion of its contents. The scolecite is stated to be the rudiment of the fertile cup, to

itself

It is



FIG. 26.-Scolecite. After De Bary.

above remarks must be received as historical, and as illustrating the nearest approach which some of the best observers have obtained towards establishing sexuality in the higher Fungi, such as Hymenomycetes and Ascomycetes.

The Gasteromycetal Fungi also include a small family in which the receptacle assumes a cup shape, especially in the genera Cyathus and Crucibulum ; but here again there is great divergence in the character of the fructification. In the latter genera the cups are at first covered with a tympanum or membranaceous veil, and when this is ruptured, are seen to contain a small number of lentil-shaped bodies, which are attached by a slender elastic cord to the inner surface of the cup. These are the peridiola which enclose spores produced upon basidia within the firm interior (Fig. 27).

46

THE FRUCTIFICATION

The excipulum, or cup-shaped receptacle, is also the form which is assumed in some genera of the *Sphaeropsideae* in which the external resemblance is again to that of the Discomycetes. The cups are sessile, often erumpent on the stems of herbaceous plants, and externally smooth or covered with bristles—for example, in *Excipula*, *Discella*, and *Ephelis*, and many others. The spores are produced on short sporophores which grow side by side from the inner surface of the receptacle, as the asci are produced in *Peziza*, but without forming a compact hymenium.

From these brief notices it is evident that fructification of widely diverse types may be found to be produced within

receptacles which are open above and therefore cup-shaped. The most prevalent form is the ascigerous, in which the sporidia are produced in asci, packed closely side by side and forming a compact disc, as in the Discomycetes. An analogous genus is found in Hymenomycetes, in which the spores are produced upon basidia, as they are in Corticium. Amongst the Gastromycetes the cupshaped receptacles enclose lenticular peridiola which con-



FIG. 27.-Crucibulum vulgare. Gard. Chron.

tain basidiospores. And in *Sphaeropsideae* certain genera with an open, cup-shaped receptacle produce naked spores, or conidia, upon short sporophores. To these might be added also, from the Uredines, the "cluster-cups" of *Aecidium*,

which contain globose spores developed in chains (Fig. 28); and possibly the *Hysteriaceae*, in which the receptacles are often closed and elongated, but in some instances are gaping in moist weather, so as to expose a compact disc of parallel asci, combined with paraphyses, after the manner of *Peziza*. This



FIG. 28.—Pseudoperidia of Aecidium.

family falls intermediate between those with a cup-shaped receptacle and the following group, in which the receptacle is a closed perithecium, but inclined more towards the former than the latter. It will be observed, in examining more closely into the morphology of these groups,

that the preponderance of species which possess a cup-shaped receptacle are sessile on the mycelium, without the intervention of a carpophore, in the sense to which we have here limited that term.

We pass now to the representatives of that large mass of Fungi in which the receptacle is wholly closed, with the exception of a terminal pore, as included under the general term *perithecium* (Fig. 29). In all essential features the fructification is the same under the two forms in which it presents itself, the ascigerous and the stylosporous. The former is that of the Pyrenomycetes and consists of cylindrical sacs, or asci, with linear paraphyses intermixed and packed closely side by side. In this respect the fructification resembles that of the Discomycetes, only that the disc, or upper surface, is not

exposed, and hence not compacted. The asci contain four or eight or sometimes an indefinite number of sporidia, which are either hyaline or coloured, and simple or variedly septate. The summit of the ascus



FIG. 29.—Perithecium and section.

is normally imperforate. Exceptional instances could be cited in which the ascus encloses but one or two sporidia, or where no paraphyses can be detected. Up to the present no clue has been found to the fertilisation of the sporidia, whether by the fertilisation of the entire receptacle in its earliest stage or that of the sporidia. In the case of some of the *Perisporiacei*, after the contact of two hyphae, a process is evolved from each, which ultimately develops respectively into oocyst and antheridium. De Bary from this traced the history of a conceptacle in *Erysiphe* to its completion; and expressed the opinion that the perithecia and asci of many of the *Ascomycetes* originated, and were perfected, in the same manner.

Other perithecia, with the same external form, habit, and texture, but with stylosporous fructification, are included systematically in the *Sphaeropsideae*. There are no asci and no paraphyses present, but the receptacles enclose an indefinite number of sporules, which are generated singly at the apices of very short slender threads. These some have called *basidia*, but that is a misnomer, since in the Basidiomycetes it is accepted with a different interpretation. In the *Sphaeropsideae* the delicate supporters of the sporules are simply sporophores. The sporules themselves do not differ materially in form, size, and appearance from the sporidia which are generated in asci, and there is a suspicion that some of them are genetically connected, but in what manner has never been ascertained.

In some genera the perithecia are nearly obsolete where the species are immersed, or else they are so fused with the

matrix as not to be distinguishable, or they may be quite spurious, so that cavities in the matrix perform all the functions of perithecia (Fig. 30). The latter condition prevails in the *Melanconieae*, where the conidia are produced, as in the *Sphaeropsideae*, on short conidiophores within definite cavities



^{IIG.} 30. — Spurious perithecium of *Mel*anconium.

or cells, the walls of which are differentiated from the matrix. There is a basal cushion or spore-bed which is formed from the mycelium, and this spore-bed originates the conidia. Saccardo and the majority of systematists apply the term "conidia" to the spore-like vesicles of the *Melanconieae* as well as to the *Hyphomyceteae* or moulds.

A small but interesting group of Fungi, having the habit and appearance of moulds, differ from them very materially in possessing a receptacle at the apex of the carpophore, which

is technically a sporangium. This apical receptacle is delicate, membranaceous, and often transparent, enclosing a number of small spores or zoospores. The mucors develop only spores within the sporangia, but the Peronosporaceae sometimes produce only passive conidia at the ends of the branchlets, in which case they belong to the naked-spored group, to be alluded to shortly, in consort with the moulds; at other times sporangia are produced, or analogous organs, the contents of which are differentiated and escape from the vesicle as zoo-These are the only instances known in Fungi in spores. which the hyphae support a delicate inflated vesicle containing spore-bodies capable of germination. This is not the only feature in which they differ materially from the moulds which they superficially resemble; but in the mycelium they differ in the hyphae being for the most part without septa, and further, in the power which they possess in forming special branches on the mycelium, which conjugate and form zygospores. These latter are able to pass through a period of rest, as resting spores, and form a second form of fruit for the mucors; as oospores are produced on the mycelium of the Peronosporaceae by a similar sexual act, and are a second form of fruit for that family, capable of passing the winter as resting spores.

Having disposed of the several forms of fructification which are to be found developed within special envelopes, or receptacles, according to their kind, we have still to deal with those less common forms in which the fructification is naked on the carpophores, and destitute of any kind of receptacle. The most typical of this system of fructification is that exhibited by the moulds, or Hyphomycetes, in which the carpophore or conidiophore is either simple or branched at the apex, and the spore-bodies, or conidia, are produced singly or in clusters at the apex of the conidiophore, or at the tips of its branches, or diffused in any other manner upon its surface. It may at once be admitted that in these nakedly-disposed spore-bodies we are unable to recognise any symptoms of sexuality, and hence they can scarcely come under any other designation than that of reproductive buds, or if that term is objected to, then as asexual spores. If we accept as an example Verticillium agaricinum, the carpophore is an erect,

50

THE FRUCTIFICATION

septate hypha, proceeding as an assurgent branch from the mycelium. In its upper portion it produces, at intervals, branches one, two, or three, at the same level, and these again produce branchlets in whorls of three. Each branchlet is surmounted by an ovate conidium, or sometimes two or even

three together. This, therefore, is a mould, with somewhat of a dendroid habit, with verticellate branches and branchlets pro-Take as ducing terminal naked conidia. another example the common mould, Penicillium glaucum, or any other Penicillium (Fig. 31): the erect carpophore divides at the apex into a cluster of short branches, and each branch is terminated, not by a single conidium, but a series of conidia, attached end to end in a chain, each conidium falling away successively as it attains maturity. In other genera the carpophore is very short and unbranched, either terminating in a single spore or in a chain of spores, but



FIG. 31.—Conidiophore of *Penicillium*.

the principle is the same—that of naked conidia borne direct by the carpophore, without receptacle.



We can only recognise in the Uredines a modification of the same principle, which is most strongly manifest in *Phraqmidium* (Fig. 32). The teleutospores consist of an elongated simple carpophore, surmounted by a multiseptate spore-body, and there is no It is similarly manifest in receptacle. Uromyces and Puccinia, for the teleutospores have a distinct pedicel, which bears the fruit and is the carpophore. In some other genera it is less manifest, whilst in Aecidium and Raestelia the distinct receptacle is of the cup-shaped series, open above.

FIG. 32.—Teleutospores of *Phragmidium*.

In all the instances given in this chapter we have denominated the bearer of the fructification by the general term of "carpophore." This is by no means

intended to ignore the fact that even as spore-bodies, having the function of spores, may be designated specifically as spore, sporidium, sporule, or conidium, so also the carpophore may, in some cases, more fitly be called a basidium, sporophore, or conidiophore.

CHAPTER VI

FERTILISATION

THE methods by which fertilisation is accomplished in many forms of Fungi remain still as great a mystery as ever, and they have only in a comparatively few instances been demonstrated for certainty. It is not so very long since that all the lower cryptogamia, at the least, were supposed to be reproduced asexually; but this is known to have been too hasty a conclusion, for the algae present many remarkable instances of sexual reproduction. In Fungi the examples have been more isolated, and in some cases still require more certain confirmation, so that it must be confessed, when such an immense number of species are taken into account, the instances in which sexual reproduction has been determined are exception-One-fourth of the total number of described species ally few. consists of those which are classed as incomplete Fungi, and hence out of consideration; whilst another one-fourth consists of the Hymenomycetal Fungi, and if these are to be excluded, then one-half are at once to be declared asexual. To these we shall be compelled to add the Ascomycetes, as without established evidence. In fact, it is doubtful whether one-fortieth part of the total number of species can be characterised as possessing Hence the opinion is now very general that sexusexuality. ality is entirely wanting in all the higher forms of Fungi, and is only to be found in small families. In this respect Fungi, as a group, are in strong contrast to Algae.

All previous efforts to establish sexuality in the Hymenomycetes having failed, Worthington Smith endeavoured again in 1875 to prove it from the Agaricini, and his observations were made on a minute species of *Coprinus*. He says that at

first the Fungus is composed wholly of simple cells; no differentiation is seen in infancy when the gills are first formed, but the basidia and cystidia come into existence only simultaneously when the plants approach maturity. This differentiation he distinctly regards as sexual, the basidia representing the female and the cystidia the male organs. When the contents of the basidia and the cystidia are interchanged, he says, the result is a return to another series of cells, which go to form a new plant. The cystidia are more sparingly produced, and at first cannot be distinguished from the basidia, though frequently larger, commonly granular within, and sometimes crowned with granules, but sometimes with four spicules. Subject to moisture, these spicule-crowned cystidia germinate at the four points, and produce long threads, which bear at their tips the granules which are so frequent in typical cystidia. The "granules" at first are not capable of movement, but they are in reality spermatozoids possessed of a fecundative power, and after the lapse of a couple of hours begin to revolve, and ultimately swim about with great rapidity. These spermatozoids attach themselves to the spores, pierce the coat, and discharge their contents into the substance of the spore. From twenty-four to forty-eight hours after this the spore discharges a cell, which soon becomes free, and this is the first cell of a new plant, which rapidly produces others of a like nature. At first the spermatozoids are perfectly spherical, when they merely oscillate, then they revolve slowly, and, as time goes on, a single turn of a spiral makes itself visible, and the bodies whirl round with great rapidity. At intervals the motion entirely ceases, and then, after a short lapse of time, the gyration is again continued. Judging from the presence of the eddy round these bodies whilst whirling, they are possibly provided with cilia, but from the extreme minuteness of the bodies themselves it is not easy to demonstrate their presence. The whirling of the spermatozoids is so strong that when they attach themselves to the spores they twist them round, after the manner of the revolving oosphere in Fucus. It is also stated that in many cases the cystidia fall out from the hymenium, and in company with the spores, and that it is upon the moist earth that fertilisation is gener-

54

FERTILISATION

ally carried out. The last observation, if verified, is rather strange, as the spores, when fallen, must be regarded as fully matured; it seems to be rather an anomaly that a mature fruit should be fertilised, rather than when in an immature condition. This much, then, has been related by Smith in a very circumstantial manner, and from it he argues that in the Agaricini the cystidia produce the spermatozoids, by means of which the spores are fertilised, either upon the hymenium, or after they have fallen to the ground. During twenty years we have not heard that his observations have been confirmed, or that the question has been set at rest.

Long before the above investigations Oersted claimed to have discovered a sort of conjugation in the filaments of the



FIG. 33.-Development of sporocarp in Podosphaera. After De Bary.

mycelium of Agarics, but this is now regarded as an error of observation.

In 1872 C. H. Peck supposed that he had found in a species of *Agaricus* "spores produced in globose asci, borne on a thick, tapering, penetrating peduncle, twelve or more spores in the ascus." This again was doubtless a faulty observation, for other mycologists failed to find the asci on the gills of the specimens determined and furnished by the original observer. M. de Seynes subsequently attributed the assumed asci to cystidia, and the supposed sporidia to external and internal granules. Hence it may be affirmed that none of the supposed processes of fertilisation in Basidiomycetes have been confirmed, and until that is done they must be regarded as asexual.

Another one-fourth of the total number of species of Fungi
is occupied by the Pyrenomycetes, in which the sporidia are developed in asci; but, so far as we are aware, it is only in the family *Perisporiaceae* that sexual fertilisation has been suggested—*i.e.* in *Erysiphe* and *Eurotium*, by De Bary and supported by Tulasne. In *Erysiphe lamprocarpa* the perithecia are produced where two filaments of the mycelium cross each other (Fig. 33). They swell slightly, and each emits a process resembling a branch. That from the lower filament soon becomes



FIG. 34. - Development of Eurotium repens. After De Bary.

oval, and is constricted by a septum from the hypha, becoming a distinct cell, which De Bary calls "oocyst." The process from the upper filament adheres closely to this cell, and elongates into a cylindrical tube, which terminates obtusely at the apex of the cell. This also is divided by a septum from the parent hypha near the base, and another towards the apex cuts off a short terminal cell, which is supposed to be the antheridium. After this eight or nine new tubes spring up around the base of the oocyst and closely applied to it, which gradually develop into the wall of the perithecium. In the

FERTILISATION

meantime the contents of the cell, or oocyst, are being differentiated into an inner wall and the contained ascus. The perithecium gradually acquires its brown tint, with the formation of sporidia in the ascus and the rooting filaments at its base, and is then complete. In other species of *Erysiphe* oocysts and antheridia are produced in a similar manner.

The formation of perithecia in *Eurotium* is analogous (Fig. 34). The generative filaments twist together at their summit like a corkscrew, generally presenting six turns closely united to each other and forming a hollow body. Then follow the production of a multitude of cells in the central cavity. De Bary thinks it not impossible that at this time some act of fertilisation takes place, but there is not even as much evidence in favour as is adduced in the case of *Erysiphe*, and hence it remains as a guess.

The opinion of De Bary may have some weight, but it is insufficient without the evidence, which thirty years following has not produced, in support of this conclusion—that "the phenomena which take place in Erysiphe authorise us to presume that in others of the Ascomycetes, having isolated perithecia, the stroma which encloses several conceptacles, or even the organs of fructification in the Discomycetes, the Tuberaceae, and other groups, are also the products of a sexual generation." There is an abundance of instances in which pyrenomycetous Fungi have two, three, or four distinct kinds of fructification, but from this fact alone nothing can be concluded as to the process of fertilisation or the existence of sexuality.

In the Discomycetes, with its four thousand species, the suggested examples of sexuality are but very few, and these have not been confirmed. Woronin examined *Lachnea pulcherrima*, and succeeded, as he thought, in recognising that the receptacle derives its origin from a short and flexible tube, thicker than the other branches of the mycelium, which is soon divided by transverse partitions into a series of cells, since denominated a "scolecite." He seems also to have assured himself that there is always in proximity to this body certain filaments, the curved branches of which, like so many antheridia, support their extremities on the "scolecite." This contact would appear to communicate to the scolecite a special

vital energy, which is immediately applied to the production of the filamentous tissue on which the disc is later to be borne.

Tulasne found the scolecite readily in Ascobolus furfuraceus, but failed in tracing fertilisation; but he was rather more successful with Pyronema melaloma, in which he found that the



FIG. 35.—Scolecite. After De Bary.

scolecite is certainly a lateral branch of the mycelium (Fig. 35). This branch is simple, or forked at a short distance from the base. and its diameter generally exceeds that of the filament which bears It is soon bent and it. often elongated in describing a spiral, the irregular turns of which are lax or compressed. At the same time its cavity is divided into eight or ten cavities.

Sometimes he had seen this special branch terminated by a crosier, and interlocked with the bent part of an analogous crosier terminating a neighbouring filament. In other cases the growing branch was connected by its extremity with that of a hooked branch. These contacts, therefore, seemed rather accidental than constant. There was, however, no room to doubt that the scolecite was the habitual rudiment of the fertile cup.

The most complete observations were those on *Pyronema* omphalodes. The globose vesicles, or macrocysts, which are the beginning of the fertile tissues—each of them emits from its apex a cylindrical tube, always more or less bent in a crosier shape, so that the vesicles resemble so many tun-bellied, narrow-necked retorts filled with a roseate plasma. Out of the same filaments are produced elongated clavate cells, named paracysts, which soon exceed the macrocysts in height,

58

FERTILISATION

and seem to carry their summit so as to meet the crosiershaped appendages, and they are soon united two and two. The union or meeting of the extremity of the crosier tube with the neighbouring paracyst was a constant fact, which he had observed a hundred times, and leisurely during a few months. There is no joining of these cells except in the very limited point where they meet, and there may be seen a circular perforation at the end, defined by a round swelling. Elsewhere they may be very near together, but they are always free from any adherence whatever. One thing can be



FIG. 36.-Formation of zygospore in Mucorini. After De Bary.

affirmed—that the conjugated cells, especially the larger, wither and empty themselves, while the upright tubes, which ultimately constitute the asci, increase and multiply.

As to the "scolecite," so called, there can be no doubt that some such bodies have been seen, but their significance has been misinterpreted. It is probably the first distinction of the fertile from the sterile hyphae, and in no sense represents the female organ.

The above will suffice for the Ascomycetes; and we have left to us the Phycomycetes, as containing the most decided and definite examples of sexuality amongst the Fungi. The Mucors, in species already investigated, develop zygospores from the hyphae of the mycelium (Fig. 36). A short clavate branch is produced from each of two neighbouring hyphae. These branches approach each other by their apices until they touch, and are called the suspenders. They contain an abundance of

protoplasm, and gradually enlarge, until they resemble a spindleshaped connective of the two hyphae. A septum is soon formed across the suspenders near the upper extremity, cutting off a discoid cell from each, which are separated from each other at the point of contact by the original wall of the conjugating suspenders. This division soon becomes perforated, and at length disappears, leaving the twin discoid cells united into a subglobose central cell, which is to become the zygospore. The membrane thickens, becomes warted and of a dark colour, nearly black, when it reaches maturity, and in this condition it settles to a period of rest.

In the family of Saprolegniaceae the oogonia, or female cells, are terminal on short branches of the mycelium (Fig. 37).



60

FIG. 37.-Oogonium with After De Bary.

They are globose cells, the membrane of which is soon perforated, and at the same time the contents are differentiated into rounded little spheres which float in the interior. From the pedicel of oogonia, or from neighbouring the hyphae, short curved branches arise, which bend towards the oogonia. These are the antheridia, which become slightly swollen at the apex, and closely applied to the wall of the oogonium. About two oospheres of Achlya. the time when the gonospheres are formed each antheridium projects into

the cavity of the oogonium one or more slender tubes, but these appear never to open or discharge their contents, so that they cannot fertilise the gonospheres, which, however, soon acquire a cellulose membrane, and the process is complete. This is the general character of the sexual reproduction, modified somewhat according to the genera and species.

Another family, the Peronosporaceae, possesses an asexual system of reproduction much resembling that of ordinary Mucedines, but parasitic on living plants. The mycelium, which permeates the tissues, usually in the autumn produces oogonia, which arise from swellings of the mycelial tubes. These take the form of globose cells, which become divided off at the base by a septum (Fig. 38). Other branches swell at the

FERTILISATION

extremity and become clavate, to form antheridia, and one of these applies itself by the obtuse extremity to the face of each oogonium. With this development the contents of the oogonium become aggregated into a spherical form in the centre to constitute a gonosphere. A slender tube is projected from the applied end of the antheridium into the oogonium until it reaches the gonosphere, when it ceases further growth. After this contact the gonosphere becomes invested with a membrane of cellulose. Its subsequent progress, as it becomes mature, is to develop a thick brown epispore, and then come to rest during the winter months.

In the Entomophthoraceae, or fly moulds, the process of



FIG. 38.-Sexual organs of Peronospora. After De Bary.

sexual reproduction is more simple. They are produced by slightly varying modes, as a result of the conjugation of opposite threads. These hyphae, either within or without the body of the host, produce lateral outgrowths at opposite points of two different threads, which meet midway between the two conjugating cells, and coalesce. The intermediate walls are absorbed, and a connecting tube is formed, through which the contents are mingled (Fig. 39). A gemma is produced on the connecting canal, which increases rapidly, appropriating the contents of the two conjugating cells to form a zygospore. After this the empty hyphae disappear. This process may be slightly modified in different species, but it follows the same principle, and the mature zygospore passes into a period of rest.¹

This much is known of sexual reproduction in Fungi: that ¹ Vegetable Wasps and Plant Worms, by M. C. Cooke (1892), p. 11.

in the *Phycomycetes* two bodies are formed, or two specialised cells come into contact, and the result is a zygospore, which is



FIG. 39.—Conjugating hyphae in *Entomophthora*.

nearly always a resting spore, as a consequence of fertilisation. In the Discomycetes it is suggested that in its earliest stage the elements of the future cup, or receptacle, become fertilised by contact with specialised filaments which represent antheridia. In the *Perisporiaceae* special processes are affirmed to be emitted from two adjacent hyphae, which are supposed to become respectively oocysts and antheridia, and from their contact to result in the production of fertilised In the whole of the perithecia. Basidiomycetes no definite mode of fertilisation has been confirmed. And for the rest, we seek for evidence in vain.

In Tilletia, a genus of the Ustilagineae,¹ peculiar phenomena undoubtedly take place in the conjugation of promycelial spores, but this can scarcely be interpreted as an act of fertilisation. The facts are simply these: when the spore germinates it produces a promycelium, a germ tube, which gives origin to bodies called primary sporidia, or, more properly, promycelial spores (Fig. 40). "A very remarkable feature about these 'primary sporidia' is that they almost invariably conjugate in pairs; that is, adjacent pairs become organically united by a short tube growing from one and becoming blended with the other, thus placing the protoplasm of the two sporidia in direct communication. In some instances conjugation takes place before the primary sporidia break away from the promycelium. After conjugation a slender germ tube is formed, which receives all the protoplasm from the two united sporidia, and if developed upon the proper host plant, penetrates into its tissues and forms a mycelium, which in turn produces a new crop of resting spores. In some

¹ Monograph of British Uredineae and Ustilaginae, by C. B. Plowright, London (1889), p. 88.

FERTILISATION

species the process is more complicated : the germ tubes produced by the primary sporidia after conjugation give origin to secondary sporidia; these in turn produce germ tubes capable of penetrating the tissues of the host and giving origin to resting spores."¹ Similar cases occur in Ustilago.

Tulasne was rather sanguine when he wrote² that assiduous observation, and the perfection with which microscopes are

constructed will have enabled the botanists of this age to determine that there are no really agamic plants-that is, without sex. At any rate they can from the present time suspect with foundation that in all vegetables, no matter to what group they belong, there exist two distinct orders of reproductive organs, the relative values of which may be compared to that of the two sexes in animals. Until latterly, however, the Lichens and Fungi seemed to form ex- FIG. 40.-Tilletia in germination. After ceptions to this rule, for all



De Bary.

the researches of phytologists could not discover in them that duality of organs which, after having been for so long the exclusive privilege of cotyledonous plants, has since been found to belong to nearly all cryptogams. Experience and investigation of forty years have shown that Lichens and Fungi still remain practically exceptions to the rule of sexuality.

> ¹ Massee, British Fungi-Phycomycetes, etc. (1891), p. 166. ² Comptes Rendus, vol. xxxv. (1852), p. 841.

CHAPTER VII

DICHOCARPISM

By the term expressed in the heading to this chapter we intend to indicate such species of Fungi as present two distinct forms of fructification, presumably proceeding from the same mycelium or vegetative system, and hence pertaining to the same species. It is contended that the word "dimorphous" would have expressed this, but we cannot assent, because that word vaguely distinguishes the organism to which it is applied as having two forms, which might apply to the fruit, to the carpophore, or to any other organ, whilst we desire its restriction to such Fungi only as exhibit two forms of fruit. There are a very large number of Fungi which might be brought under this designation, and those would fall into three groups. (1) Those which produce two forms of fruit from the same stroma or mycelium. (2) Those which are reputed to possess two forms of fruit, the genetic connection of which has not yet been (3) And those which produce two clearly demonstrated. forms of fruit successively or alternately, by an alternation of generations.

We shall attempt to give only a few illustrations of the first kind—those which produce two forms of fruit from the same stroma or mycelium—which will be sufficient to make clear the purport of our definition, and the first shall be selected from a genus in which probably all the species are dichocarpous. *Hypomyces* is one of the genera of the *Pyrenomycetes* which grows upon dead Fungi, chiefly the *Hymenomycetes*, in broadly effused patches, the mycelium of which is partly innate. The woody Fungus *Fomes annosus* may sometimes be found with a white mycelium running over the hymenium and penetrating

DICHOCARPISM

Upon this mycelium erect branches are the substance. developed and form conidiophores, having the habit and appearance of an ordinary mould. The conidiophores branch several times; the branches, usually three, form a whorl, and these again are similarly branched in whorls, the branchlets being each terminated by three shorter branchlets in a whorl, each branch and branchlet being attenuated upwards. The terminal branchlets bear one or more small oval conidia. This has been called Verticillium microspermum. Upon the same mycelium grow a number of ovate perithecia, which are clad with a dense short wood; and when mature they contain numerous asci, each enclosing eight lanceolate uniseptate sporidia. This is Hypomyces broomeanus, of which the above mould bears the conidia. Hence this species is dichocarpous, one form of fruit being the mould, and called the conidia, the other the Sphaeriaceous Ascomycete with asci and sporidia.

Maple leaves will furnish another example in the wellknown pitchy blotches which are so common in autumn as to attract every eye. These black patches, which are closely adnate to the leaves, are the stroma of Melasmia acerina, as it is then called. The perithecia are cells immersed in this stroma, which contain small hyaline curved sporules borne on short slender sporophores. After these leaves have fallen on the ground and lie in damp places during the winter, another form of fruit is developed within the same stroma; but in this instance the sporidia are developed in asci and are nearly ten times as long as the sporules, thread-like and flexuous. The stroma itself becomes more corrugated, and splits irregularly to allow the sporidia to escape. In this state it is called Rhytisma acerinum, but the two forms are one species, with a stylosporous and an ascigerous form of fruit, and the latter is never matured until the leaves have lain for some time upon the ground.

We may select the living leaves of the hedge maple to furnish our next example, which can be found in summer in any hedgerow. At this time the leaves are covered or blotched with white, as if they were whitewashed, but seen under a microscope this appearance is caused by a dense mycelium of white threads adhering to the surface of the leaf. From these threads arise short erect branches, which become constricted

65

5

at short distances, and then divided into cells; as they mature the apical cell falls away as a conidium, and then the next, and the next, in succession, until exhausted; this is *Oidium aceris*, or the conidial stage of the Fungus which speedily succeeds it. Little black dots appear to the naked eye to be sprinkled over the white mycelium in the autumn. These are the conceptacles which contain the later fruit, forming little dark brown peridia of a nearly globose shape, and are attached by delicate threads to the mycelium. Externally the conceptacles are ornamented with a number of projecting threadlike appendages, curled, or divided and curled, in both directions at their tips. Internally the conceptacles enclose eight asci, each holding eight sporidia. In this condition it is known as *Uncinula bicornis*, of which the *Oidium* produces the naked conidia.

We may refer incidentally to some Discomycetes, on the authority of Tulasne,¹ who states that in *Ocellaria*, which occurs



FIG. 41.—Bulgaria inquinans. in little tubercles on the twigs of trees, a great number of the tubercles, which ought to be transformed into cup-shaped receptacles, do not pass into this perfect state until after having produced very short, narrow conidia, or spermatia, as he calls them, or else stylospores on short sporophores, such spores being equal in size to the true sporidia to be afterwards developed. Some of the tubercles confine themselves to this stylosporous generation, and always remain simple "pycnidia" — that is to

say, tubercles or cells enclosing stylospores. The normal and fully-developed tubercles assume a cup shape, and contain eight-spored asci, as is usual in the Discomycetes. The same author also cites another species, *Bulgaria inquinans* (Fig. 41), which in the adult state represents a very large, deep, black peziza, is in its extreme youth an obtuse tubercle, the whole mass of which is divided into ramified lobes, and is of very irregular form. The extremities of these lobes become, towards

¹ Tulasne, Comptes Rendus, vol. xxxv. (1852), p. 841.

DICHOCARPISM

the surface of the tubercle, recipients from which escape for some time waves either of pure spermatia or of spermatia mixed with stylospores. Both are ovoid, but the spermatia are uncoloured and much smaller than the stylospores, which are as black as the spores of a *Melanconium*. These two quotations are given as exhibiting what we have called Dichocarpism as it was presented to the view of one who accomplished very much in demonstrating the fact that the same species of Fungus is capable of developing reproductive bodies of more than one type or form.

Our next example shall be found on a dead twig of birch, bursting through the bark in black pustules almost as large as a rape seed, or rather, oozing out in wet weather like thick black ink. Examined more closely, a mycelium will be found

at the base forming a compact sporebed, on which the brown elliptical sporules grow on short sporophores closely packed together. When mature these separate from their sporophores, and ooze from the apex of the pustule in an inky mass. In this condition it is called *Melanconium bicolor*. Later in the season the same pustules will be found occupied by a cluster of perithecia, perhaps six or eight, placed almost in a circle,



FIG. 42. -Melanconis.

with rather long necks (Fig. 42). Internally these perithecia contain numerous asci closely packed together, each ascus containing eight sporidia, of an elliptical shape, divided across the centre into two cells, and known as *Melanconis stilbostoma*, one of the compound *Sphaeriacei* of which the *Melanconium* bore the naked conidia, so that we have the same stroma yielding naked stylospores, and afterwards sporidia enclosed in asci. An endless variety might be adduced of ascosporous Sphaeriacei having also a preceding crop of stylospores on the same mycelium.

Here we may cite two examples of another kind which are described in another chapter. These are—the Mucors, which bear erect fertile branches surmounted by inflated vesicles

containing spores and producing from the same mycelium branches which conjugate and form a zygospore; also *Peronospora*, the branched carpophores of which sustain zoosporangia, and from the mycelium produce, sexually, resting spores or oospores.

Dead box leaves are often to be met with bearing on their under surface little pink tufts of a delicate mould arising from a creeping mycelium. Sometimes the fertile hyphae are effused, and not tufted. The conidiophores are shortly branched, with the branches in whorls, bearing at the tips of the branchlets rather spindle-shaped conidia, and then called *Verticillium buxi*. Subsequently from the same mycelium erect branches form fertile threads, which are themselves sparingly branched, and bear at their apices small globose sporangia, each enclosing several minute gonidia. This condition is *Mucor hyalinus*. It is nevertheless doubtful if there are any conjugating branches which form a zygospore, and which would in that event have been a third form of fruit, but this condition has never been observed.

The above examples will be sufficient to indicate some of the forms which, for the want of a better name, we have called dichocarpous Fungi. They might as truly have been called dimorphic. In the first we had a Mucedine, or mould, arising from the same mycelium or vegetative system as a Pyrenomycete. That is to say, the same vegetative system produced two forms of fructification, one having the attributes of a mould with naked conidia, and the other an Ascomycete with sporidia enclosed in asci. The second instance was that of a black effused stroma or cushion-like expansion with the appearance and attributes of one of the Sphaeropsideae, producing within cells the sporules on short sporophores characteristic of the family; but later on the same cells gave origin to sporidia, of which every eight were enclosed in asci, and the Fungus was in all respects a Rhytisma, one of the Ascomycetes. In the third we had a naked mycelium, the erect branches of which produced in chains the conidia of an Oidium, or white mould; but at a later period the same mycelium developed the perithecia of an Erysiphe. In the fourth instance the pustules of a Melanconium gave origin to the conidia characteristic of the genus

DICHOCARPISM

on short sporophores; but, mixed with these, later on appeared the perithecia and ascospores of a compound Sphaeria, an Ascomycete. In the fifth we had a Mucor producing spores in terminal sacs, and, by conjugation of other branches, zygospores. In the sixth a Peronospora with terminal zoosporangia on branched hyphae, and oospores upon the mycelium. Lastly, a mould, bearing conidia on the branches, and afterwards from the same mycelium a Mucor with inflated terminal sacs enclosing spores. All these are examples of a second form of fruit produced from the mycelium of the first.

We have now to indicate briefly those species which are reputed to possess two forms of fruit, the genetic connection of which has not yet been clearly demonstrated. It may be premised that there are a large number of cases in which an association of this kind has been suspected, but it is needless to cite more than two or three. In the summer the leaves of Rumex are often marked on the under surface with mealy white spots, seated upon discolored blotches of the green leaves. These spots are caused by a white mould with a short and simple, rarely branched conidiophore, supporting at the apex a single elliptical conidium, attached obliquely; this is Ovularia obliqua. In the autumn the same plant, and often the same leaves, will present similar spots, which do not carry the mould but clusters of very minute perithecia, half immersed in the leaf. These perithecia contain cylindrical asci, each enclosing eight oblong uniseptate sporidia. It is supposed, and with some good show of reason, that the mould constitutes the conidia of this Sphaerella rumicis, but the connection does not appear to have been definitely established. We have observed the two on the same leaf, but not on the same spot.

The leaves of horse - radish (Armoracia) are often seen covered with whitish circular blotches, upon which are sprinkled a number of minute black dots, the partially immersed perithecia of a species of *Phyllosticta*, having minute sporules on slender sporophores. Later in the year similar spots on leaves of the same plant are occupied with perithecia of almost identical appearance, but containing the asci, hitherto immature, of a supposed *Sphaerella armoraciae*. There is no evidence of the relations subsisting between the two Fungi,

only a suspicion that the one is a form of the other. Many species of *Phyllosticta* growing upon living leaves, as well as some species of *Septoria*, are supposed to be in some way related to corresponding species of *Laestadia* and *Sphaerella*, but their association has never been determined.

There is scarcely a more common mould on dead herbaceous plants than Cladosporium herbarum, which forms dark olive patches with a velvety appearance, consisting of flexuous jointed hyphae and a profusion of long elliptical conidia, at first simple, and then uniseptate, proceeding from a creeping mycelium. There is often to be seen, in close proximity, or even mingled in the same patches, others with similar but shorter threads and much larger conidia, which are broadly elliptical, and not only many times septate, but the cells are again divided at right angles, so as to appear muriform. This is Macrosporium commune. Some have conjectured that the one species passes into the other, which is hardly probable; others that there is some occult connection between them; and it has been intimated that both forms of mould are only conidial states of a common Sphaeria, with coloured muriform sporidia, known as Pleospora herbarum. This is another example of supposed dichocarpism that rests more upon supposition than ascertained fact.

Without indicating any particular species, it is generally believed that the species of *Phoma*, which consist of perithecia enclosing small hyaline sporules borne on short threads, and so common on nearly every dead twig or herbaceous stem, are each related to some ascosporous Fungus of similar appearance. This is probable in at least a great number of instances, but demonstrated in only a few. What are called "imperfect Fungi," such as *Sphaeropsideae* and the Hyphomycetes, are so called from the impression that they are not autonomous, but simply forms or conditions of other species. Hence, if the combined total of these species is accepted at eleven thousand, there must be an immense number of dichocarpous species of which we are still in ignorance.

The last section of this subject includes the species which produce two forms of fruit successively, or alternately, by an alternation of generations. Although included here for con-

DICHOCARPISM

venience, these are scarcely to be considered as dichocarpous. The definition would be that each generation or form completes its career in the same form as it commenced, so that each starts from a germ, and the cycle is not the career of a single individual, but of a series of individuals which revert to the original form after one, two, or more intermediate and different generations. This phenomenon is certainly not common in Fungi, but it is illustrated in the Uredines, where the series consists not only of two but of several generations which intervene between those of a like denomination. We will take a supposititious example, admitting the facts for the sake of illustration. The leaves of pear trees are not uncommonly visited by a Fungus called Raestelia cancellata, in which a cluster of peridia appear on a yellow spot. When mature these peridia discharge a profusion of subglobose warted brown spores. This ends the first generation by the production of spores. According to some these spores are drifted from the pear leaves to a juniper bush, where they germinate and invest the bush, producing, as a result, what is assumed to be the same Fungus, in a different form, upon a new host. In this case gelatinous cylindrical masses burst through the bark without any peridium, consisting of elongated, two-celled, hyaline spores on long pedicels, all agglutinated together by the gelatine. This is the second generation, different from the first, but ending in the production of spores, called specially teleutospores. In the next stage these teleutospores germinate, and the germ tube produces as buds small promycelial spores. which are carried by the wind or otherwise back to the leaves of a pear tree, producing thereon either directly or indirectly the peridia of Raestelia cancellata, and so the reversion is made to the original form, after the intervention of an intermediate generation as Gymnosporangium sabinae. Thus, then, Raestelia cancellata on pear leaves produces subglobose brown spores, and these germinating produce Gymnosporangium sabinae, with hyaline uniseptate teleutospores on the savin, which is the second generation. The teleutospores of the Gymnosporangium, through the intervention of promycelial spores, reappear on pear leaves as a Raestelia, and thus the first form of fruit is reached again after the intervention of a different generation.

First generation *Raestelia*, second generation *Gymnosporangium*, third generation *Raestelia*, fourth generation *Gymnosporangium*, and so on alternately, constituting an alternation of generations. Technically, there is but one species appearing under two forms, and the two names represent two conditions of the same Fungus.

Another illustration may be found detailed in a succeeding chapter, in which another Uredine is traced through the Aecidium-form, the Uredo-form, and the Puccinia-form, reverting to the Aecidium-form in the fourth generation. It will be observed that alternation of generations differs materially from what we have designated dichocarpism, because in the former a single generation produces but one form, and the second generation proceeds directly from the germination of the first, and consequently upon a new mycelium. In the latter, dichocarpism, both forms of fruit are produced from the same mycelium, and belong to one and the same generation. We have also seen that the number of forms which are possible to a single species are not confined necessarily to two, but may extend to three or four, whilst the principle remains the same. Hence we conclude that the same species of Fungus is capable of producing, on the basis of its own vegetative system, two or more forms of fruit, one of which, but not both, may be the result of sexual fecundation.

CHAPTER VIII

SAPROPHYTES AND PARASITES

THE student will not proceed far in the investigation of the nature and relations of Fungi before he is called upon to recognise the distinctions between saprophytes and parasitesthe species which thrive upon the decay and cause the disintegration of dead matter, and those which infest and flourish upon the tissues of living plants. Saprophytes are numerically in preponderance throughout the Fungi as a whole, and represent those forces of rejuvenescence which build up from the ruins of an old life the forms of a new generation. They are not only the agents in disintegration, but the immediate consequences of the phenomena of decay. Dead wood, leaves, fruits, herbaceous stems, and every fragment of dead vegetable matter, and in some degree of animal, are capable of developing and supporting new vegetable forms which utilise and assimilate the chemical products of decay, and inaugurate a new cycle of activity. In this relation Fungi have been called the scavengers of vegetation, since if they are powerful in the work of destruction, they are also the ready agents in regeneration. The method by which these results are accomplished is somewhat uniform. If a dead log or only a chip of wood lies upon the ground in a damp situation, it soon becomes permeated by the delicate, imperceptible threads of Fungus mycelium; with the penetration of these threads the component cells of the timber become more and more dissociated from each other, a kind of fermentation softens the material, and it is not long before the whole mass has become friable and crumbles at a touch. Before this crisis is reached, and whilst the mass still adheres together, the Fungus mycelium gives further evidence

of its vegetative vitality, and produces here and there external nodules, which are the commencement of efforts towards reproduction. In a comparatively short period of time the surface of the log is decorated with young Agarics, effused patches of Corticium or Poria, or other forms of Hymenomycetal Fungi. Fully thirty-five per cent of the known species of Agarics are developed in this manner from decaying wood and leaves; and of the remaining sixty per cent, allowing five per cent for other contingencies, it may fairly be assumed that a large proportion flourish at the expense of the dead roots, vegetable humus, indistinguishable fragments and remains of vegetation which are present in the soil, or the dung of animals which are vegetable feeders. If we turn from the Agaricini to other of the great groups of the Hymenomyceteae, such as the Polyporei and the Thelephorei, we shall be still more convinced of the great, almost overwhelming, preponderance of species which manifestly flourish upon the remains of previous vegetation. Of the 9600 known species of Hymenomycetal Fungi, really parasitic species are almost, if not wholly, unknown.

Although numerically inferior to the saprophytes, the parasitic Fungi are none the less important, from the sad havoc they are capable of producing amongst cultivated plants. A little experience will soon demonstrate that the parasites are of two kinds-namely, those which establish themselves externally upon the green parts of growing plants, and do not penetrate the tissues; and those which are developed internally, deeply seated in the tissues of the infested plants, and not making their appearance externally save for the purpose of fructifica-The former may be called epiphytal, growing upon plants, tion. and the latter endophytal, growing within plants, which may be illustrated by familiar examples. Common epiphytal parasites are-the various species of the Erysiphei ; such as the Sphaerotheca castagnei, or hop mildew; the Sphaerotheca pannosa, or rose mildew; the pea mildew, or Erysiphe Martii; the mildew of the maple, Uncinula bicornis; and many others. These all appear upon the leaves of living plants in thin effused white patches, which give the appearance of being dusted with flour. There are two stages or conditions of the parasite, and both associated with the web-like mycelium. The earliest stage

SAPROPHYTES AND PARASITES

consists solely of the delicate threads which branch and interlace each other, and form a thin white film of mycelium, sometimes on one and sometimes on both surfaces of the leaves, to which they adhere by means of little projections, or haustoria, which enter the stomata. From this mycelium arise shorter and thicker threads, consisting of a chain of oval cells, each of which falls away consecutively from the apex, and becomes a conidium capable of germination. It is these fallen conidia which mainly give the mealy appearance to the patches. In former times they were treated as autonomous Mucedines, and were included in the genus Oidium. Later in the year these same white mouldy patches, when examined with a pocket lens,

will be observed to be sprinkled with little globose bodies, which are at first yellow and subsequently dark brown approaching to black. These are the perithecia, not larger than small pins' heads, attached at the base by delicate filaments of mycelium (Fig. 43). When FIG. 43 .- Erysiphe lampromature, the membranaceous coat splits irregularly at the apex, and exposes the



carpa, with ascus and sporidia.

contents, which consist of pear-shaped asci, or sacs, each enclosing two, four, or more elliptical hyaline sporidia, which also are capable of germination and constitute the ascigerous fructification of the Erysiphe. From this brief description it will be evident that this parasite is entirely superficial, or epiphytal, and that the injury it inflicts is caused by obstructing the healthy action of the leaves and, in a manner, killing them When applying external remedies for plant by suffocation. diseases, such as fungicides, it should first be clearly ascertained whether the parasite is or is not epiphytal, since fungicides are more likely to take prompt effect when application can be made to them direct, and, by removing obstruction, restore the healthy action of the leaves. Our commonest vine disease, which attacks the leaves and fruit, is of the present character, although only the conidial condition is accurately known.

True endophytal parasites are more varied in their character, and consist primarily of the "rotting moulds" - Fungi which have the habit and appearance of Mucedines, but with a more

complex fructification. The disease which has for some years attacked the potato, and at one time was called the "potato murrain," is of this character. This disease is unfortunately present, and deeply hidden in the tissues of the plant, before any external evidence is manifest. When the fructification appears, usually on the under surface of the leaves, it occurs on vaguely circumscribed patches, which become discoloured and soon rot away. The mycelium pervades the entire plant more or less, but especially at the point of issue. The erect conidia-bearing threads issue singly or in bundles through the



FIG. 44.—Stages of germination of a conidium or sporangium of *Phytoph-thora*. a, ripe condition; b, contents breaking up into blocks; which escape, c, d; as zoospores, e; with two cilia, f, g; zoospores at rest, g, h; and germinating, i, j, k. After Marshall Ward.

stomata, soon becoming branched towards the apex once, twice, or several times in a furcate manner, the tip of each ultimate branch bearing a single oval or elliptical hyaline conidium, or, in the present case, a sporangium (Fig. 44). When mature these sporangia, for the most part, become granular within, and at length the granules accumulate in definite spots, and finally become invested with a delicate membrane; so that when the parent membrane ruptures and the contents escape, they do so in the form of an uncertain number, it may be four or six minute rounded bodies, each furnished at one end with a pair of delicate movable hairs. As soon as these are liberated and they encounter a thin film of moisture, they float away, being

SAPROPHYTES AND PARASITES

impelled by the vibrating hairs, as if endowed with animal life, hence termed zoospores. Thus it will be observed that some of the species of *Peronospora* differ from the true moulds in that the threads do not bear veritable conidia but sporangia, which contain numerous active zoospores which escape on the rupture of the parent cell and float off on their own account. The ultimate career of these zoospores is usually brief, for after floating a short time they settle down to rest, the cilia or hairs fall away, and a thin germ tube is projected, which enters a neighbouring stoma in the leaves of the foster plant, and originates a new mycelium, and thus extends the action of the parasite. There is, however, another mode of reproduction which takes place within the tissues of the foster plant, by a differentiation of the mycelium and the production of oospores, a kind of resting spores, which hibernate through the winter and provide for the continuance of the parasite in the spring. These oospores are of considerable size, and possess a thick coloured outer coat, and they remain embedded in the old stems, haulms, petioles, or leaves of the host-plant, quiescent throughout the winter, and are only liberated by the decay of the tissues. In the spring, and when uninfected young seedlings of the host-plant may be supposed to be numerous, these oospores awaken to activity, the contents become divided in the same manner as the contents of the conidia were divided, only much more numerous; then the thick outer coat is ruptured, and a great number of active zoospores emerge, ready to be washed by the spring rains into favourable positions for germinating and infesting new plants. In this manner the parasite is preserved through the winter, and the perpetuation of the species assured. Whether the zoospores are derived from the sporangia, which are developed on the aerial branches of the hyphae, or whether derived from the resting spores, their subsequent history and functions are the same-that is to say, entering the host-plant by means of a germ tube, developing a new mycelium, and producing a new infection. Some species of the Peronosporaceae produce simple conidia on the hyphae, which never develop active zoospores, but germinate at once. Although, as has been shown, infection may proceed from without inwards, the subsequent manifestation of

77

vegetation and reproduction proceeds from within outwards, and hence these Fungi are *endophytal*.

The life-history of some other types of endophytal parasites is still incomplete. Amongst Mucedines we may instance *Ramularia*, with some allied or analogous genera, in which the mycelium pervades the tissues of living plants, and ultimately hyphae break through the cuticle, and produce conidia in the air; such conidia, having the power of germination, penetrate the host-plant, and cause a new infection. In the *Melanconieae* the species of *Gloeosporium* produce a plentiful mycelium within the living plant before localised spore-beds are formed beneath the cuticle, which latter at length is ruptured and sporules escape, and these are also capable of germination and the origination of a new mycelium.

The Hypodermeae are, however, amongst the most potent of endophytal parasites, and of these the Uredineae are almost ubiquitous. Perhaps no Fungi have been studied more persistently or closely than these, so that the literature would fill volumes. We shall only select a typical instance from the genus Puccinia, as the readiest method of elucidation. The one which attacks almost all the species of violet, Puccinia violae, will answer the purpose. First of all discoloured spots are observed on the leaves, and then upon these spots small convex elevations, which are ultimately rather darker in colour and punctured; these are the spermogonia, which enclose the minute bodies to which the name of spermatia has been applied, without any clear idea of their functions, except that they always are associated with the cluster-cups or aecidia that appear simultaneously or soon afterwards. Sometimes the spermogonia are seen on the upper surface of the leaves, with the aecidia on the under; or both may be on the same surface, with the spermogonia in the centre and the cluster-cups surrounding them. In the present species the aecidium appears in the form of an orbicular spot on the leaves, or an elongated mass on the swollen and distorted petioles; on the leaves the spot is yellowish, and the cluster-cups are densely packed upon it, almost touching each other, the margin torn, whitish, and turned back like a fringe. Within these cups the aecidiospores are bright orange and in chains, separating themselves at the

SAPROPHYTES AND PARASITES

apex when mature, and then globose and warted. This stage was formerly known as Aecidium violae. Before either spermogonia or aecidia appear there is always present a plentiful mycelium in the tissues. The swelling of the petioles is caused by the development of this mycelium, the cluster-cups being developed from the same mycelium as the spermogonia, and consequently deeply innate and thoroughly endophytal. The mature aecidiospores, after voluntary separation from the chain, will germinate within a few hours, but seldom after a period of forty-eight hours. Each spore has several germ-pores, perhaps four or six, but germination seldom proceeds from more than one. This cylindrical tube continues growing until it has acquired a considerable length, the coloured contents of the spore passing meantime along the tube to its extremity, which finally enters one of the stomata of the proper hostplant, and there, by branching and progressive growth, constitutes a mycelium, presumably the mycelium which becomes the spore-bed of the uredospores. If we return to the violet leaves later in the year, we shall find the under surface of many leaves exhibiting small raised pustules, which are scattered all over the surface. These sori, or pustules of the Uredo, are soon exposed by the irregular splitting of the cuticle, and the light brown spores, resembling snuff, are freely distributed. Examined more closely, each pustule will be found to possess a spore-bed of compacted mycelium, from which the uredospores grow, at the apices of rather short hyaline threads or peduncles, which are soon absorbed, leaving an elliptical pale-brown spore, with a shortly spinulose surface, as the second stage of an alternation of generations, the problematic spermatia being left out of the question. It must be remembered that the origin of an uredospore-bed is not absolutely resultant from a germinating aecidiospore, but it may also be produced by a germinating uredospore, or by the germination of a promycelial spore. This fact may be associated with the other fact, that some species of Puccinia are known with which no aecidium has yet been associated. The mature uredospores have two, three, or four points of germination or germ-pores. The germination takes place, as in the aecidiospores, within a few hours, and in like manner the growing point enters one

of the stomata of the host-plant, where it becomes the new mycelium of a spore-bed, which may either be that of a uredospore or a teleutospore.

The violet leaves which display on their under surface the pale-brown scattered pustules of the uredospores, will, later in the season, exhibit also similar pustules mixed with them, and nearly of the same size and form, but much darker in colour, or the leaf may be occupied entirely with these darker pustules, which contain the teleutospores. Seen under the microscope, these spores of the third generation will be found to differ from the aecidiospores and the uredospores in being two-celled —that is to say, they are divided across the centre by a transverse septum into two superimposed cells of a somewhat hemi-



FIG. 45.—Germinating teleutospore of *Puccinia*. After Tulasne.

spherical form, supported upon a longer and more persistent hyaline pedicel. They are produced, like the uredospores, from a spore-bed of mycelium arranged more or less compactly side by side. The apex of the upper cell has generally a more or less conspicuous hyaline nipple in the centre. In this species the coat of the spore is smooth, but in some others it is warted or spinulose (Fig. 45). The mature teleutospore may germinate almost immediately, or in some species only after a con-

siderable period of rest, in which latter case they are practically resting spores. The germ tube from either cell, projecting through the germ-pore, is at first a simple tube into which the contents of the cell pass, and retreat to the upper end, which continues to grow and become a promycelium. The extremity becomes divided off from above downwards by one or more septa, and then each compartment sends off a short pointed branch, which is soon dilated at the point. This expanded end then assumes an oval or kidney shape, and receives the contents of the compartment to which it belongs. In the course of a few hours these new bodies are abstricted, and become promycelial spores,

SAPROPHYTES AND PARASITES

which soon fall away. The germination of teleutospores results therefore in a promycelium, which develops small secondary or promycelial spores, and these latter are ready to germinate at once. When these promycelial spores are placed on the damp surface of the leaves of the host-plant they germinate, and the growing point enters one of the stomata, where it forms a mycelium, the contents of the promycelial spore passing down the tube, whilst the empty spore-case soon This new mycelium may produce spermogonia falls away. and aecidiospores, thus reverting to the original point of departure; or it may give rise to a crop of uredospores, without the intervention of aecidiospores; or it may produce teleutospores, which are functionally alike or unlike the parental teleutospores from which the promycelium was derived. Throughout all these mutations there is no divergence from the endophytal character of the parasite, which is of a peculiar and characteristic type. Here, then, we have in brief the typical life-history of one of the Uredineae-the teleutospores in some instances being unicellular, and then Uromyces; or bicellular, and then Puccinia; or multiseptate, and then *Phragmidium*; the character of the teleutospore determining the generic name to be applied to the cycle.

There have from time to time been suggestions of hereditary transmission in Uredinous infection, but as the frank acceptance of such a possibility would weaken the effects of such results as are claimed to follow upon artificial cultivation, the advocates of heteroecism ignore as much as possible all suggestions of hereditary transmission. Analogy nevertheless favours the probability of inheritance, and some few stubborn facts seem to support this view. Some years since we had occasion to examine some celery plants, the leaves of which were badly attacked by Puccinia, whilst other plants in the same garden did not show a single diseased leaf. Upon inquiry it was found that the diseased plants were raised from seed which had been derived from plants badly diseased at the time, but that the healthy plants were reared from seed which had been saved from plants without trace of disease, either in the past year or in their progenitors of preceding years. The foliage of all the diseased plants was destroyed, and no disease appeared

81

in that same garden, upon celery plants, during the succeeding ten years. The inference certainly must be that the seeds contained, in some occult manner, the germs of the disease, transmitted in this way from generation to generation, and not obtained by local infection of the seedling leaves, from germinating promycelial spores. If the latter had occurred, then the infection would not have been confined to plants descending from infected parents, whilst other plants growing within less than three feet did not show a spotted leaf; but both series of plants would, on the contrary, have suffered in an equal manner.

Another case is related by Mr. Worthington Smith, wherein he says it is common to find hollyhock seedlings showing the Puccinia on their seed leaves. This he had traced to the presence of pustules of the disease outside the seeds or carpels, of which he gave a detailed account in the Gardener's Chronicle. Yet another instance is upon record, in which a well-known nurseryman had imported Dianthus seeds direct These seeds were carefully grown under glass, from Japan. and, immediately they were up in the seed-pans, they were all attacked and destroyed by the characteristic Puccinia. On making a microscopical examination of a series of these seeds mycelium was detected inside the integument which surrounds the embryo, or infant plant, and within the coat of the seed. Another and equally conclusive incident has been narrated by the Rev. M. J. Berkeley, in which plants of Pyracantha, raised from seeds imported from Russia, were all killed by a species of Fusicladium, or black mould, whilst old plants of Pyracantha, growing at the same place, remained perfectly free from disease. In this last instance we have corroborative evidence, in which the parasite was not a Uredine but a mould; and the doctrine of inheritance in plant disease is demonstrated to have taken place with other parasitic Fungi, and is not confined exclusively to Uredines. It is sometimes objected that these instances cannot be referred to hereditary transmission, but that they are simply cases of the transmission of a perennial mycelium. That does not appear to alter the fact of transmission, for if the parent transmits disease to its offspring, the disease is inherited from the parent, whether it has been transmitted by germs or hyphae.

SAPROPHYTES AND PARASITES

It was at one time regarded as a reproach to those who studied these endophytes that in very many cases the species were named after the usual host-plant, and it was only necessary to know the host to be able to name the parasite without trouble or examination. At the present time it is held to be true that the promycelial spores will not enter by their growing point, or infect in any way any other plant except the one. two, or more species of phanerogam upon which it customarily grows. Such being the case, it was not so very foolish after all to combine the name of the host with the endophyte; and even now we are disposed to doubt if the old grouping of species, according to the affinities of the supporting plants, was not more effective, practicable, and sensible than the more recent, more complicated, and more unnatural system of the present day. This, however, is not a point to be discussed here, inasmuch as it is altogether a question of classification, when reduced to practice, and belongs to a subsequent chapter.

CHAPTER IX

CONSTITUENTS

THE chemical composition of Fungi varies considerably as to quantitative proportions in different families, and, to a less extent, in different genera and species. The larger Fungi, which constitute the Hymenomycetes, are those which have generally been submitted to analysis. Of course water is a considerable element in fresh specimens of fleshy Fungi. The highest percentage is about 90 per cent, and the lowest about 9 per cent, the latter being that of a woody *Polyporus*. Perhaps a reasonable mean for Agarics would be about 60 or 70 per cent.¹ Taci gives the following analysis of *Russula foetens* :—

Weben					. 67.0
Water		•			. 0.6
Mannite		1	•	•	. 4.6
Fibrin (Albuminoids)			•		1.00
Gum					. 1.5
Fungin or Cellulose					. 20 [.] 0
Fat .					the second se
Ash		•	•		. 5.13
					00.51

Acids, etc. undetermined.

The substances allied to sugar are mannite and trehalose, the latter found in ergot, and elsewhere. Albuminoids are some form of fibrin or albumen, and distinguished by containing nitrogen as well as carbon, hydrogen, and oxygen. These substances are valuable as food, the nutritive value being in great part indicated by the percentage of nitrogen. This percentage is high in Fungi, higher in dried Agarics than in peas

¹ Fistulina hepatica contains 86 per cent of water.

CONSTITUENTS

and beans. The special kinds of albuminoids are not determined, but they closely resemble those found in animal food. The cell walls consist of meta-cellulose or fungin, but there is no lignin or woody fibre. Some gummy substance and oil or fat occur in most species. Mineral salts are found as ash on burning. The ash or mineral matter varies from 19.8 in *Psalliota arvensis* to 3.0 in *Fomes fomentarius*, calculated on the dried plant.

Vegetable acids of various kinds have been named in connection with Fungi, as citric acid, malic acid, fumaric acid, oxalic acid—Hamlet and Plowright found 083 per cent in *Fistulina hepatica*—and oxalate of lime or potassium is by no means uncommon.¹ Agaricic acid has been found in *Polyporus* officinalis. Other acids of a special nature may be found in particular species. Some Fungi contain free acetic acid. A substance called Fungic acid is mentioned by earlier observers, but this is stated to be a mixture of citric, malic, and phosphoric acids.

The colouring matters of Fungi are still open to investigation, and especially so by the aid of the spectroscope. By this means four yellow or orange matters have been determinedphycoxanthine, which is yellow; pezizaxanthine, which is the orange colour of Peziza aurantia; and two colours related to xanthophyll, or the yellow colouring matter of leaves. Phipson obtained a red colouring matter from Cortinarius violaceus, and Stahlschmidt a substance which constituted 43.5 per cent of the dried Fungus, from what is supposed to have been Poria purpurea. This substance has been termed "polyporic acid," and is soluble in alkalis, with an intense violet colour. Certain species of Boleti, notably Boletus luridus, contain a yellow colouring matter which becomes blue on exposure to the air. Phipson asserted that this was a derivative of aniline, although neither aniline nor its salts have this property. Stewart² suggested that indigogen was a yellowish substance which is

¹ Crystals of oxalate of lime may often be seen upon the surface of the pileus of *Polyporus sulfureus*. Oxalic acid in some form has been detected in scores of species of Hymenomycetes. Hamlet and Plowright mention a great number (*Journ. Chem. Soc.*, 1877).

² Stewart, Alkaloids in Fungi. Trans. Woolhope Club (1883), p. 119.

86

converted to blue on exposure to air, and possibly the colouring matter was indigogen in Boleti. He obtained this pigment, and found that it rapidly passes from yellow to blue, and from blue to brown. While in the blue state it can be again reduced to yellow; but when it has once become brown it seems to be destroyed, as the blue colour could not by any means be restored. The blue matter contains neither indigo nor aniline. From this it will be seen that he was not successful in determining this colouring matter in *Boletus*. It is not by any means certain that this colouring matter, whatever it may be, has any relation to the toxicological properties of the Fungus, as has been generally supposed, although its development is strong in poisonous species.

Very little can be said of the nature of the odours which pertain to Fungi, but Stewart has made some suggestions in this direction. He says that the volatile alkaloid called *tri-methylamine* is a colourless liquid with a powerful fishy odour, and is, in fact, the cause of the smell of decayed fish; it is found also in the flowers of the hawthorn, and in some Fungi, as in ergot of rye and putrefying yeast. He also hints at the possibility of the odour of *Phallus impudicus* and that of *Clathrus cancellatus* being derived from the same source. There are some Agarics which possess the odour of putrid fish, but they are small and not common, hence the source of odour is unknown.

The toxicological ingredients of Fungi have been investigated several times, but the results have hardly accorded in any two cases, and are still open to inquiry. Böhm has especially studied *Boletus luridus*, and found large quantities of choline, together with a substance similar to cholesterin, small quantities of muscarine, and luridic acid, which crystallises in brilliant red needles, and yields succinic acid on distillation. Essentially the same substances were found in *Amanita pantherina*, but in that the acid crystallises in yellow crusts.¹ The Fly Agaric (*Amanita muscaria*) yields two alkaloids muscarine and amanitine. Muscarine is a strong narcotic, and in some respects antagonistic to atropin. Amanitine is identical with the animal bases choline, mentioned above in *Boletus luridus*, and with neurine. An eminent physician and

¹ Journ. Chem. Soc., 1885, p. 1008.

CONSTITUENTS

surgeon has informed us that upon one or two occasions he successfully employed hypodermic injections of atropin in cases of Fungus poisoning. The effects of the amanita on the human subject are singular. "At first it generally produces cheerfulness, afterwards giddiness and drunkenness, ending occasionally in the entire loss of consciousness. The natural inclinations of the individual become stimulated. The dancer executes a *pas d'extravagance*, the musical indulge in a song, the chatterer divulges all his secrets, the oratorical delivers himself of a philippic, and the mimic indulges in caricature. A straw lying in the road may become a formidable object, to overcome which a leap is taken sufficient to clear a barrel of ale or the prostrate trunk of an oak." The symptoms are endless in variety, and justify the arrangement of these agents, toxicologically, with narcotico-acrid poisons.

It is now conceded that glycogen, or "animal starch," is not confined to the animal world, but is also found in Fungi. The asci of the Ascomycetes are completely permeated with it, and at first it is diffused throughout the whole of the young plant, but soon accumulates in the asci, where it is utilised in the development of the spores.¹ It has also been found in the Mucors, in some cases throughout the mycelium and the young sporangia, especially in *Phycomyces*. The greater part of it is taken up by the protoplasmic contents of the spores.² The same authority has found it also in the Basidiomycetes. By tracing the passage of glycogen from one part of the plant to another he convinced himself that it plays the same part in the economy as starch in other classes of plants, and that it is the first visible product of the absorption of carbon. It is usually most abundant towards the base of the Fungus, in the vicinity of the soil. Its quantity is greatest at early periods of growth of the Fungus, gradually disappearing with growth, probably from the effect of respiratory combustion.³ It has been found plentifully in Peziza vesiculosa, in truffles, and in Phallus impudicus. Errara contends that glycogen plays the same part in Fungi that starch does in other plants. It is not

Journ. Roy. Micr. Soc., vol. ii. (1882), p. 824.
 ² Ibid., vol. iii. (1883), p. 397.
 ³ Ibid., vol. v. (1885), p. 504 ; vol. vi. (1886), p. 833 ; vol. viii. (1888), p. 96.

formed, like starch, from the free carbon-dioxide of the atmosphere, but out of previously existing organic carbon compounds, especially the products of the decomposition of other food materials. Examination of the ergot of *Claviceps* has shown that the oily material is changed into glycogen in the same manner that oily material is converted into starch in germinating seed. There is a special accumulation of glycogen in the capitulum of the young Claviceps.

The varnished appearance of the pilei in some of the species of Fomes, such as Fomes laccatus, Fomes australis, and others, is affirmed by Dr. Wettstein to be due to a secretion of The special hyphae are of peculiar form, thickened resin. above clavately, and containing when young an oily yellow Eventually protuberances appear at the end of the fluid. hyphae, which gradually increase and exude a cap of resin. These exudations flow together and form a continuous coat.¹ A yellow resin has been found by Zopf in Polyporus hispidus, which exudes when fresh a plentiful supply of yellow juice like a pigment, which stains paper of a gamboge yellow. Zopf reports that there are two substances: one is the yellow resin, which is insoluble in water, but otherwise resembling gamboge; the other a soluble yellowish-green pigment with The same author states that the bright acid properties. red colour of Polyporus cinnabarinus is due to the mixture of a substance which forms beautiful cinnabar-red crystals, denominated xantho-trametin, and also a resin.² In some specimens of exotic species of Fomes we have sometimes seen flakes of resin on the pileus which could be chipped off, but could never be satisfied how they came there-whether from the tree trunk which supported the Fungus, or as an exudation from the Fungus itself. The varnished pileus of Fomes nigrolaccatus becomes quite sticky soon after the application of spirit to the surface. Fries mentions Polyporus resinosus as exuding a resinous juice, and it is quite possible that some of the woody Polypori which grow on coniferous trees will secrete a considerable amount of resin, as they have a tendency to become laccate when old.

Journ. Roy. Micr. Soc., vol. vi. (1886), p. 486.
 ² Bot. Zeit., vol. xlvii. (1889), p. 54, etc.

88

CONSTITUENTS

The latex of the Hymenomycetes¹ is of variable composition, and especially of three types, of which the most numerous examples are to be found in the genus Lactarius, which is evidently resinous. There is also the Mycena type, which is confined to a few species of Mycena, and the Fistulina, which is rather more fluid and contains tannin. The latex tubes are large compared with the neighbouring tissue, and much branched, having occasional septa, enclosing a turbid, granular fluid variable in colour. In most species of Lactarius the greatest number of tubes occur in the subhymenial layer and the periphery of the stem; the former branches in one direction into the hymenium, and in the other into the tissue of the pileus. In Mycena the system is more simple, and the tubes are extremely long, running through the periphery of the stem and ending in the pileus. In Fistulina hepatica the tubes are distributed through the entire receptacle, and are not collected in definite spots, with very few in the hymenium. The milk is persistently white in Lactarius piperatus, vellereus, and many others, sometimes acrid, and in other species quite mild. In Lactarius scrobiculatus, theiogalus, chrysorrhaeus, etc., it is at first white, then becoming yellow. In L. deliciosus it is at first deep yellow, and then green. In L. aspideus and L. uvidus the milk, which is white at first, becomes lilac. In Lactarius acris the white milk turns reddish, and in Lactarius fuliginosus of a dark yellow, approaching reddish. Not only does the latex differ in colour, in volume, and in taste, but also in consistency. In some it is creamy and sluggish, and in others watery, slightly coloured, and flowing freely. All these features indicate a variability in composition. The character of the yellow juice of Peziza succosa appears to be unknown.

The phenomenon of phosphorescence has been so long known in Fungi and so often alluded to, that only a brief reference is necessary. Several Agarics have this property of which the largest number, for any locality, have been met with in Australia. All of them are species found growing upon dead wood, and all have white spores. Nearly the same story is related of all of them—to the effect that they emit a light

¹ Journ. Roy. Micr. Soc., vol. vi. (1886), p. 833 ; vol. vii. (1887), p. 627.

90

sufficiently powerful to enable the time on a watch to be seen by it. The effect produced by it upon the traveller, when on a dark night he comes suddenly upon it glowing in the woods, is startling; for to a person unacquainted with this phenomenon the pale, livid, and deadly light emanating from it conveys to him an impression of something supernatural, and often causes no little degree of terror in weak minds or in those willing to believe in supernatural agencies. The kind of light emitted in all cases is described as shining with a pale, livid, and greenish phosphorescent glow.¹ This luminosity is not confined to the Agarics, but may be witnessed in those cord-like Rhizomorphs which run through rotten wood or bark, and are common in mines. The thin mycelium which traverses rotten wood in every direction, under favourable conditions exhibits the same Recent observations have determined that in peculiarity. some cases luminosity is produced by species of bacteria. Yet, under all these conditions and manifestations, the cause of the light is still as much of a mystery as ever, despite all suggestions as to its originating in some connection with phosphoric acid.

This is merely a chapter of hints and suggestions which might have been considerably extended, but it will be recognised that in many cases there is no satisfactory explanation at present to be given for the phenomena alluded to. There is still ample work for the chemist, but it is not remunerative, and in many instances necessarily one of much labour and Fungi are themselves so putrescent that their assiduity. examination must be commenced at once, when they are collected; besides, it is not always that a sufficient supply for investigation can be obtained at one time. When we learn that 50 lbs. of Agarics are required to obtain a quarter of an ounce of muscarine, and that the same quantity of Boletus luridus is necessary to obtain from it any alkaloid it may possess, or discover truly the source of the blue colour, we are not sanguine as to much advance in this direction.

¹ Romance of Low Life amongst Plants, by M. C. Cooke, London (1893), p. 208.

CONSTITUENTS

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¹ It has been considered advisable to give only a brief bibliography to this and the succeeding chapters, of the most important works only, or those accessible in the English language.


PART II

CLASSIFICATION



CHAPTER X

FUNGI IN GENERAL

CONCISE and accurate definitions are difficult to construct, and seldom remain long without gathering about them numerous exceptions. This is especially the case in botany or zoology, where the continual accession of knowledge gradually renders old limitations untenable. All the definitions in vogue with old authors have one after the other been swept away, and many of those which succeeded them are either gone or going. Even the old distinctions between plant and animal are no longer to be trusted, and subsidiary divisions are either diffuse or vague. In the lower Cryptogamia there has been a great shaking amongst the dry bones, so that when Algae, Lichens, and Fungi are spoken of they no longer convey the same absolute ideas which the same words represented only half a century Whether the hypothesis associated with the middle of ago. these three terms is tenable or not, the affinities between Lichens and the Algae on the one hand, and with the Fungi on the other, have been shown to be very intimate, and the difficulties of delimitation increased.

We have only to concern ourselves directly with Fungi, and here the difficulty of concise definition soon becomes manifest. We need not go back beyond the year 1835, when Berkeley contributed a short introduction to the fifth volume of Smith's *English Flora*, edited by W. J. Hooker, in which he defined Fungi as " plants, consisting of cells and fibres, always springing from organised, and generally decayed or decaying, substances, not perfected when immersed in water, bearing reproductive sporidia, either externally or internally, naked or enclosed in variously formed cells, many of which frequently

concur in the reproduction of a single individual." This is not a very neat definition, and not wholly accurate. " Not perfected when immersed in water" is contradicted by the Saprolegnieae, which flourish in water. In a footnote to the same volume the subject is alluded to in the following terms :---"It is almost impossible to draw up characters which shall in every case distinguish the three orders of Lichens, Algae, and Fungi. Indeed, the more natural such orders are, the more difficult it is to arrive at anything approaching to mathematical precision. Thus, in general, Algae grow in water; Lichens in air, drawing their nourishment from the medium which surrounds each respectively, and not from the matrix; while Fungi are nourished by dead or decaying organised matter, and have therefore been styled Usterophytae. Yet, true as these facts are in general, there are a few instances in which to a certain extent they will be found incorrect according to the letter." But a very large number of Fungi are not "nourished by dead or decayed organised matter," but flourish upon and destroy living organisms, both vegetable and animal. The most compact definition was that which described Algae as cellular aquatic plants which derive their sustenance from the water in which they grow; Lichens as cellular plants growing in the air, and deriving their sustenance from the surrounding medium; and Fungi as cellular plants which obtain their sustenance from the matrix on which they flourish. This was the basis of the definitions given by Berkeley in his Introduction to Cryptogamic Botany, published in 1857, wherein he defines the Algals as "Thallophytes deriving nutriment from the water in which they are submerged," and the Mycetales, including both Lichens and Fungi, as "Thallophytes deriving nutriment from the matrix or the surrounding air; mycelium more or less evident." Subdividing the latter, we have Lichens described as "aerial, nourished by air and not by the matrix, producing gonidia"; and Fungi as "hysterophytal or epiphytal, nourished by the matrix, never producing gonidia." If we proceed to apply the last definition-for we are not concerned with the others-to the whole mass of organisms now generally grouped under the Fungi, we shall discover that it is inadequate.

96

The most recent definition of Fungi with which we are acquainted is that given by Saccardo in 1889: "Cryptogamic plants, cellular, destitute of chlorophyll, for the most part having a mycelium, either parasitic or saprogenous, for the most part aerial." That is to say, they are "cellular cryptogamic plants, chiefly developed in the air, either epiphytal or saprophytal, and mostly with a mycelium, but destitute of Recognising the difficulty in constructing a ehlorophyll." definition which shall approach to mathematical precision, we may accept the above as the nearest approach to accuracy which ingenuity has yet devised. Considerable emphasis has generally been placed on the presence of a mycelium in the larger majority of Fungi, as the analogue of the protonema of mosses and the thallus of Lichens. The analogy, however, is imperfect, and rather superficial in most cases, since a true mycelium is almost a thing by itself.

The gill-bearing Agarics, such as the common mushroom, have a conspicuous filamentous mycelium, from which the stem arises, and which permeates the matrix to such an extent that, in a compact form under the name of "bricks," it constitutes the medium through which cultivation is maintained. This mycelium or spawn, although only produced artificially in the case of a single species, is universal to a greater or less extent in the Hymenomycetal Fungi. In a certain sense it is the representative of the root in flowering plants, but may be better regarded as the vegetative system of the Fungus. During the winter, in terrestrial species, this mycelium remains in the soil in a hibernating condition, so that a crop of the resultant Fungi may be looked for in the succeeding year. It is an open question what portion of the Fungus crop in any given year should be referred to a perennial mycelium, and what portion to the germination of the spores of the previous year's crop. Some mycologists contend that in the majority of instances, as in the commoner species, the continuity is maintained by means of the mycelium. We have observed in the case of Agaricus (Flammula) carbonarius, which occurred plentifully on charred ground not under cultivation, that, the ground not being disturbed, the same Agaric made its appearance regularly for four or five years, and then rapidly declined

in size and number until it disappeared. When the latter condition occurred, all traces of the carbonisation of the soil had long vanished, and it was overrun with docks (Rumex), which superseded and replaced the Agaric. Whilst the Agarics were in the ascendant, the soil was found, at all periods of the year, plentifully traversed by mycelium. In the case of Agaricus (Clitocybe) nebularis we have remembrance of a mass of decaying leaves, which was undisturbed for several years, and produced in succession for as many years in the autumn good crops of the Agaric. The inference would be that the mycelium was perennial, but it is not wholly conclusive, since the germination of the spores of one season might also form a new mycelium for the production of the next year's The generally-accepted theory of the growth of fairy crop. rings attributes their peripheral extension to the continued outward growth of a perennial mycelium. Experienced Fungushunters are well aware of the fact that, in the case of such Fungi as Cortinarius triumphans and Agaricus (Amanita) muscarius, they may be met with year after year in the same spot, under the same birch tree, and often in company; but this fact would not of itself demonstrate whether the appearance was due to a perennial mycelium or the rejuvenescence by means of germinating spores. It is not difficult to cause the spores of Agarics to germinate artificially in a suitable medium, but it is almost impossible to carry on the process to the formation of a proper mycelium. This, however, proves nothing as to what goes on in a state of nature, where the conditions are such as not to be successfully imitated. We may be certain that the hibernation in the Agaric does not take place with the thin-coated spores, but with the mycelial threads resulting from germination. In other orders of Fungi, and in the Algae, the resting-spores secrete a thick rigid outer coating, in which the hibernating season is passed, the conidia only, or such spores as germinate at once, having but a thin envelope. It may be inferred, therefore, that whether the inycelial threads are persistent from a previous season, or but recently developed by germination of the spores, it is under the form of mycelium, and in that form alone, that the winter is passed. Experience has demonstrated that a keen winter,

98

when the ground is not well clothed with snow, is succeeded by an autumn in which the fleshy Fungi are considerably reduced in numbers—that is to say, it is a bad Fungus year. There may be other conditions—such as general low temperature, absence of humidity, etc. — which seriously affect the latent mycelium and, as in the years from 1890 to 1893, largely diminish the production of Agarics in the autumn.

The indurated tree Fungi, such as the Polyporei, are also possessed in many cases of a copious mycelium which penetrates and disintegrates the tissues of the wood. It may be taken for granted that neither the arboreal Agarics nor the Polyporei establish themselves, or can be developed from healthy living tissue. The wood is at first dead at that particular spot, and traversed by mycelium, before there is any external appearance of the Fungus. There is no external Fungus without an internal mycelium, but there may be a very profuse mycelium and no external Fungus growth. In this connection we may indicate that condition which is popularly known as "touchwood," where the whole substance is permeated by mycelium, and what at one time was hard and firm oak or ash timber is rendered so friable that it crumbles beneath the fingers. In tropical regions immense masses of mycelium are produced from disintegrated timber, long known under the name of Xylostroma, extending for many feet and of variable thickness, with a texture resembling white leather. The conditions have all been favourable to the vegetative system rather than the reproductive. As flowering plants under exceptionally favourable conditions develop a luxuriant growth without flowers or fruit, so the mycelium of Fungi may also vegetate luxuriantly without producing organs of fructification, until the vegetative growth is checked by deficiency of humidity or some other cause. Another condition of mycelium was in past times regarded as autonomous, under the generic name of Rhizomorpha. In this instance the mycelium partakes of the character of long, branching or anastomosing, rigid cords, with a dark or black exterior, often growing between the bark and timber of dead trees, or penetrating the timber in mines. It may extend for many

yards if the conditions are favourable, and can only rarely be traced to the production of any reproductive apparatus, such as pileus and hymenium. It has been demonstrated that one form of *Rhizomorpha* may be traced to a development in *Agaricus melleus*, another form in the common *Polyporus* squamosus, and yet another in *Fomes annosus*.

The mycelium is also remarkably in evidence in the large order Hyphomycetes, or moulds, in which there is always at first a creeping mycelium of entangled threads, from which arise afterwards the erect and sometimes branched conidiophores or fertile threads, surmounted by conidia or spores. Instances will occur in which, owing to a superabundance of moisture, no fertile threads are produced and the whole Fungus consists of a mass of sterile mycelium. It is only necessary to refer to one of the forms of "blue mould," named Penicillium crustaceum, which will produce a profuse mycelium in fluids, forming an expanded felted mass resembling the substance known as the "vinegar plant." So long as there is a plentiful supply of liquid the vegetative system will go on indefinitely, but a check must take place and the supply of moisture be cut off before erect fertile threads and spores will be developed. Not only the saprophytic but also the epiphytic moulds commence with a mycelium, in the latter instance concealed within the substance of the host-plant. Thus we have characteristic examples in the genus Ramularia amongst the Mucedineae, and in Cercospora amongst the Dematicae. These have their analogues in the Peronosporaceae, formerly classed with Mucedines, but now associated with Mucoraceae as Zygomycetes.

The majority of the genera of the *Physomyceteae* are on an equality with the *Hyphomycetes* in the strong development of the mycelium; and it is in connection with this mycelium that the phenomenon of conjugation takes place which results in the production of zygospores, or resting spores, by means of which the species are preserved through the winter. This takes place not only in the *Mucoraceae*, which are mostly saprophytes, but also in the *Peronosporaceae*, which are destructive epiphytes. In the former the mycelium is more or less superficial, and in the latter innate.

In the *Hypodermeae*, which include the *Uredineae* and the *Ustilagineae*, and are consequently epiphytal, the mycelium is never absent, although innate and concealed.

The Ascomycetes, as well as the Sphaeropsideae, have possibly a smaller development of mycelium than the other orders enumerated, but it is seldom even apparently absent. In the former the Perisporiaceae furnish many examples of an abundant mycelium, which is superficial on living plants in the Erysiphei, and consequently easily recognised by the naked eye. From this cursory view it will be manifest that the mycelium is an important, and often a very prominent, attribute of Fungi.

We have not alluded to some of the smaller groups, and especially to those which are tentatively associated with Fungi, such as the *Saccharomycetes* or yeast Fungi, the *Schizomycetes* or Bacterial Fungi, and the *Myxomycetes*—which latter some authors have struggled to link with the animal kingdom—but to this we may return hereafter. Neither have we considered it necessary to allude here to those compact bodies which are morphologically dense nodules of mycelium, known as Sclerotia. They are more or less associated with all the principal orders in their ultimate fructification, and their evidence was not essential to strengthen the case.

No dissertation is required in support of that portion of the general definition which characterises Fungi as "destitute of chlorophyll." In a few instances a green colouring is present, but it is not due to chlorophyll, nor is it of the colour of chlorophyll-green, but of a verdigris or aeruginous tint. When it is contended that chlorophyll is ever present, and instances are furnished, it will be time enough to contest this point; meanwhile nothing will be gained by attempting to prove a negation.

The popular mind will perhaps seek to be satisfied with a little more general information than is to be extracted from a short definition, and to this end we may instance a few of the typical forms which are assumed by Fungi, which probably are the most variable in this particular of any of the Cryptogamia. The most efficacious manner of doing this seems to be an indication of the most salient features in the different primary

groups into which they are divided, leaving each group to be analysed and amplified hereafter.¹

Let it be remembered that there are two distinct types in which the fruit, or spores, are produced in the whole of the Fungi—that is to say, the naked spores are borne at the tips of threads or basidia, and exposed from the first or soon afterwards. This is the first type. In other cases the spores are enclosed from the first, in some definite number, within little membranous tubes or sacs called asci, and are not set free until fully mature. This is the second or ascigerous type. There is a very small intermediate group which seems to partake of the characters of both primary types—with the addition of sexual reproduction—represented by the Phycomycetes.

Let us return to the naked-spored Fungi. These we shall find to constitute three or four groups of a well-defined character, of which the largest and most important is that which includes the large fleshy or woody Fungi best known to the unscientific public as mushrooms and polypores, which have the naked spores arranged upon a special spore-bearing surface called the *hymenium*. In this group the hymenium is covered with more or less club-shaped, erect cells, or basidia, which are surmounted by two to four short spicules, or sterigmata, each surmounted by a spore. These are the Basidiomycetes, or Fungi with basidia, and were almost the whole of the

¹ I. Spores exposed, or not enclosed in Asci.

PERFECT -	(a. Hymenomycetes. b. Uredineae, etc.	Basidiospores. Spore cycle. Conidia.				
IMPERFECT	d. Sphaeropsideae.	Sporules at first produced from a hymenium, which is at first nearly covered by their receptacle.				

This group evidently belongs to the other three, as there are no asci present, but are linked to the Ascomycetes by the perithecium, excipulum, or specialised cavities in which the spores are produced.

II. Sporidia enclosed in Asci.

- a. Pyrenomycetes-receptacle perforate or ruptured.
- b. Discomycetes-receptacle discoid.
- Including Hysteriaceae—receptacle bilabiate. c. Tuberaceae—receptacle always closed.

Fungi as known to the older botanists of the time of Ray and Hudson. Another group of the naked-spored Fungi are those parasites of living plants in which for the most part there are two or three stages of existence, each terminated by a reproductive body having the nature of a spore. These are minute and pustular Fungi, popularly known as smuts, rusts, and brands, but called by scientists the Ustilagineae and the Uredineae, the spores of each generation being borne singly upon short slender sporophores. The reproductive organs are at first covered by the cuticle, which splits at maturity and exposes the naked fruit. The third group are either saprophytes or parasites, but still of minute size, and may be superficial in the former case, or innate and erumpent in the latter. The mycelium gives rise to erect threads, either simple or branched, which produce at the apex, or distributed over the branches, naked spores, either singly or in clusters, capable of germination. These are the moulds, or technically, the Hyphomycetes, which are regarded generally as imperfect Fungi, a sort of transition stage or conidia of some higher and more developed forms. The fourth group are also imperfect Fungi, and may be either saprophytic or parasitic and of minute size. In this aberrant group the majority do not produce from the first exposed naked spores, in which feature they are distinct from the three preceding groups; but the spores are enclosed within a globose or flask-shaped receptacle, which dehisces at the apex when mature and permits the spores to escape. In certain subsections the receptacle is spurious or almost obsolete. In all cases the spores are produced singly at the tips of very short threads, and are expelled when mature. These Fungi were formerly called Coniomycetes, or constituted the bulk of the Coniomycetes, but are now better known as the Sphaeropsideae and Melanconiaceae. They are so small as hardly to be visible to the naked eye, and hence have never acquired a popular name. These groups represent the naked-spored Fungi, and, it will be observed, contain only one group in which the individuals are sufficiently large to attract general attention, and still to some untutored minds represent all which they recognise as Fungi. Of the other groups, the rusts and smuts, and the moulds, are

103

partially and obscurely known, rather from their results than from their own nature.

The second type of reproductive structure is the ascigerous, in which the spores are not produced naked at the extremities of sporophores, but are enclosed within special membranaceous



FIG. 46.—Asci and paraphyses.

cylinders or sacs called asci, without sporophores, and are dispersed by rupture of the asci when mature (Fig. 46). Generally they are all included under one term as Ascomycetes, but three subdivisions are recognised as furnishing important distinctions, which may be referred to with advantage in a general purview. The largest subdivision is that in which the receptacle which encloses the fructification is always closed during growth and development, and only perforated or ruptured at maturity for the dispersal of the spores. The typical form consists of a minute, subglobose receptacle or perithecium, which may be fleshy, membranaceous, leathery, or carbonaceous, and either superficial or immersed. Externally they are often black or dark-coloured, and are seated upon a more or less distinct mycelium. In some cases a number of them are associated together, and sunk beneath the surface of a common stroma, which is consequently larger In all cases the and more conspicuous. interior of the receptacle is filled with a mass of parallel tubes, closed at each extremity, and containing normally eight, but sometimes

four or sixteen, or rarely a larger number of minute spores or sporidia. Side by side with these tubes or asci will commonly be found a great number of thread-like filaments, possibly abortive asci, but known as *paraphyses*. The upper extremity of the receptacle is sometimes elongated into a neck which is perforated, or the neck is suppressed and the apex of the perithecium is perforated to admit of the discharge of the mature sporidia. This subdivision goes by the name of the *Pyrenomycetes*.

The second subdivision of the Ascomycetes differ chiefly in the character of the receptacle, which is fleshy or leathery and cup-shaped, and only closed when very young, but soon expanded, reaching in some cases a diameter of several inches, but often much smaller or very minute. The disc, or inner surface, of these cups is compact, rarely gelatinous, and consists of the hymenium, or fruit-bearing surface, which is composed of asci and paraphyses, closely packed side by side. The great feature, then, which distinguishes this subdivision from the last is the open or cup-shaped receptacle and the exposed disc, or hymenium, and hence called the *Discomycetes*.

A small section occupies a position somewhat intermediate between these two large orders, possessing some of the characters of both. The perithecia are black and leathery or almost carbonaceous, closed at first and when dry, but opening when moist with a longitudinal fissure, and then gaping and exposing the hymenium; so that whilst it approaches the Pyrenomycetes in texture, and to some of them in the elongated mouth, it comes near to Discomycetes in the compact exposed disc, so that sometimes it has been united with one subdivision and sometimes the other. In both cases it is maintained as a distinct order under the name of *Hysteriaceae*.

In addition to all these are those subterranean Fungi, of which some are called Truffles, in which, although the spores are contained in asci, the latter are not enclosed in a perithecium, as in *Pyrenomycetes*, nor arranged in a disc, as in *Discomycetes*, but are dispersed throughout the whole substance, within folds or cavities, and are not expelled or set free, except by the decay and dissolution of the entire fabric. These are the *Tuberaceae*.

In order to complete this general survey of the chief larger groups of Fungi, we must allude briefly to a somewhat confused section, which still maintains the old name of *Phycomyceteae*, somewhat extended in its scope. It will be observed that although the spores or conidia are naked in some genera, as they are in the moulds, they are in other cases enclosed within a common membrane, suggestive of *Ascomycetes*. The feature which is relied upon for holding together this rather heterogeneous agglomeration of genera, is their sexuality, extending

mostly to the phenomenon of conjugation, and resulting in the production of zygospores. The polymorphic developments cannot be described here, so that it must suffice to say that the Mucors and the fish moulds (*Saprolegniaceae*), the rotting moulds, such as the potato disease (*Peronosporaceae*), and some other peculiar forms of Fungus structure, constitute this intermediary group.

What remains of the organisms generally grouped under the designation of Fungi are rather outside families, the relationships of which are still somewhat uncertain. Here belongs the Saccharomyceteae or yeast Fungi, although there is no room for doubt that they are correctly united with Fungi; but their aquatic habit, low organisation, and imperfect fructification justify their relegation to the lowest place. They are, doubtless, to a large extent, imperfect forms of some higher group. Similarly the microbes, or bacterial organisms, the minute Schizomyceteae, which in former times were mostly associated with Algae, find a place in juxtaposition with the Saccharomyceteae. The most aberrant group are the slime Fungi, or Myxomyceteae, which some few naturalists still claim for the animal kingdom. In the early, or vegetative, stage they certainly conduct themselves in a manner totally different from other known Fungi, assuming amoeboid forms, and uniting in a plasmodium; but in the final, or reproductive, stage they follow a completely fungoid type, and produce spores which are not to be distinguished from the spores of Fungi. Thus much is sufficient to indicate the predominant features of the chief groups of Fungi, and to demonstrate what are the kind of plants which are associated within the limits of the short definition first given of a Fungus.

In the words of one author, who gave a definition of Fungi thirty years ago, they "derive nourishment, by means of a mycelium, from the matrix on which they grow"; and this furnishes a clue to their character and functions—*i.e.* as the destructive agent in organic nature. That this is really the case, a few illustrations will suffice to carry conviction. Of the gill-bearing Fungi nearly 30 per cent grow upon decayed wood; the mycelium penetrates the tissues, disintegrates the cells, and produces a condition which we call decay, but which

is in effect reducing it to a pabulum capable of supporting the life of the Agaric which is to be developed from the mycelium. All decayed wood is more or less penetrated by Fungus mycelium, whether the Fungus itself is developed or not, the full development depending upon a sufficiency of moisture, or other surroundings. Doubtless continued moisture predisposes the wood to decay, dissolves what is soluble, softens the cell walls, and induces a kind of fermentation; the growing mycelium does the rest by slow disintegration and the liberation of the chemical constituents, so that the main factor in the destruction of dead wood is Fungus mycelium. The destructive process is extended, in like manner, to dead leaves fallen on the ground, and consequently continually moist, their final reduction to vegetable humus being expedited by the growth of Fungus mycelium. There are about 7 per cent of British Agarics which flourish habitually on dead leaves or the dead stems of herbaceous We have computed that about 64 per cent of the plants. British Agaricini are terrestrial, or nominally so, but we cannot separate those which flourish on old charcoal beds, on decaying sawdust, or vegetable humus. Undoubtedly many of those which grow ostensibly upon the ground thrive at the cost of buried vegetable matter, the sites of decayed stumps, or fragments of old roots. All we can claim for them is that all these Agarics flourish upon their matrix, deriving their nourishment from the substance upon which they grow, which must be nitrogenous, and consist more or less of vegetable or animal matter diffused through the soil, and not its inorganic constituents. Of the residue of the Hymenomycetes little requires to be said, since nearly all the Polyporei and most of the Thelephorei grow on rotten wood, which is penetrated by the Need we mention two species as pre-eminent, mycelium. Polyporus hybridus and Merulius lacrymans, both known as " dry-rot," which are in evidence for their power of destruction.

In addition to the Saprophytes are all those parasites which attack living plants and compass their destruction. There can be no doubt about the whole family of the *Uredineae*, the rust and mildew of wheat, the hollyhock disease, the plum-leaf rust —all determined foes of the plants upon which they flourish. And there are upwards of twelve hundred different species

known, which attack various plants, and some unfortunate hosts are the victims of two or three distinct species, all of which appear to defy the ingenuity of man to eradicate them. Equally disastrous in their effects, and persistent in their attacks, are the "rotting moulds," or Peronosporaceae, of which the potato disease is one form, the American vine disease another, besides many other species which are only of less importance because the plants they attack are less extensively cultivated, and less associated with the supplies of human food. No one who has had experience of any of these pests amongst his lettuces, onions, tomatoes, or in his clover field, would estimate lightly their powers of destruction. The Erysiphei also are a family of external parasites, the copious mycelium of which take possession of living leaves, and destroy by suffocation, closing and obstructing the air passages, and are thus conspicuously destructive. Those parasitic Fungi, of which a considerable number are now known, which establish themselves upon the bodies of living insects, and by the penetration of the mycelium absorb all the tissues, soon cause death, and then, in most cases, an external fertile manifestation of the parasite takes place. In like manner the aquatic moulds of the family Saprolegnieae, of which the moving cause of salmon disease is an example, take possession of fishes and batrachians, and carry on the work of destruction. There are also amongst imperfect Fungi many entire genera which attack living plants and ensure their quick destruction.

Assuming that the power and influence of the *Schizomycetes* are not exaggerated, what an agency for destruction must we recognise in the bacterial Fungi, now so wildly credited with being the cause of many of the most destructive epidemic diseases which affect the human subject, as well as inferior animals! If we only admit those which are proven beyond dispute, it is scarcely possible to estimate the full extent of the marvellous power possessed by organisms so minute in the destruction of animal, and probably also of vegetable, life. And so, as we walk through autumnal woods, we see vegetable matter all around us in a state of decay, with Fungi living and thriving upon it at the expense of the dissolving tissues, appropriating the changed elements of a previous vegetable life to

the support of a new generation, and leaving behind some of the results of disintegration to assimilate with the soil. The gardener makes, in a useless corner, his pile of the castaway twigs and cuttings of his trees and the derelict haulms of herbs and vegetables. Soon, over the whole putrescent surface, mycelium and mould proclaim the advent of a new era of vegetable activity, and anon the whole mass teems with new life. In this metamorphosis as the Fungi flourish the twigs decay, for the new life is supported at the expense of the old, until finally both destroyers and destroyed return again to the soil from whence they were derived, to form fresh pabulum for a succeeding season of green leaves and sweet flowers. What we call decay is mere change-change of form, change of relationship, change of composition; and all these changes are effected by various combined agencies-water, light, air, heat, these furnishing new and suitable conditions for the development of a new race of vegetables. But what a potent agent have all these in the myriad forms of Fungi, which, above and beyond all other conditions of vegetable life, deserve the name of the "Great Destroyer."

We have already intimated that the relationship of Fungi to Lichens is closer than to any other of the Thallophytes, as evidenced by their association, in some methods of classification, as members of a mycetal alliance. It may be useful to indicate here some of the general features in which Lichens differ from Fungi, in addition to those set forth in the short diagnosis.

Lichens are perennial; they grow very slowly, but they attain an extreme age. Some species, grown on the primitive rocks of the highest mountain ranges in the world, are estimated to have attained an age of at least a thousand years; and one author mentions, after the lapse of nearly half a century, having observed the same specimen of *Sticta pulmonaria* on the same spot of the same tree. On the other hand, the Discomycetous Fungi, which are closest in alliance, are annual, very short-lived, their whole existence being limited to a few weeks, rapid in growth and rapid in decay, not a trace of some species remaining after a few days.

Lichens will exist under conditions of aridity which no

other vegetables could support. Some are peculiar to calcareous rocks; a few are found on arenaceous rocks; many are common on the granitoid series, including micaceous, gneissic, granitic, and quartzose rocks; and *Lecidea geographica* is frequent on the smoothest and purest quartz. Fungi, on the contrary, must have moisture for their very existence, are mostly found in damp and shaded situations, and could never exist under the conditions just enumerated for Lichens.

Of all plants Lichens support extreme cold most successfully, whilst Fungi succumb at the approach of frost.

Lichens which grow upon the bark of trees may be seen flourishing in profusion during the life and vigour of the tree; whilst Fungi do not and cannot flourish on growing and vigorous bark, but on diseased, dead, or decaying spots.

Lichens obtain the greater portion of their pabulum from the atmosphere, and only their mineral constituents from the matrix. Fungi, on the other hand, obtain their chief support from the decaying vegetable matter on which they flourish, gathering up a large store of the nitrogenous results of putrefaction and decay, and disintegrating the matrix on which they prey.

Lichens in their chemical composition contain a large number of substances which are wholly unknown amongst Fungi, whereas also the most active alkaloids discovered in Fungi have no analogue in Lichens, notably those of an active poisonous character.

Lichens contain but a small percentage of water as compared with Fungi, so that in desiccation they do not shrivel, collapse, or perceptibly diminish in size; whereas Fungi shrivel up and collapse, so as scarcely to be recognised, become liable constantly to the attack of insects, or, if damp, subject to the development of mould; whilst Lichens may be preserved for years under like conditions, without fear of insect or mould.

Lichens, when collected and cast aside without the slightest care or precaution, do not exhibit the least tendency to putrefy; whilst Fungi, with the utmost care in drying, can scarce be preserved from unmistakable evidences of incipient putrefaction. It is quite erroneous to state, as some have done, that the gonidia constitute the only difference between Lichens and Fungi, whereas the presence of gonidia is only one out of many differences which exist between them.¹ The above comparison is rather suggestive than exhaustive, but it will be sufficient for our present purpose, and is intended rather for the assistance of collectors than as a help to scientific classification.

There is yet another general aspect to which we may briefly allude, and that is the recent views which have been expressed as to the evolution of Fungi. Mr. A. W. Bennett² traces all the various forms of vegetable life to three lines of descent, represented by three distinct kinds of cell-contentscolourless, blue green, and pure green. The first appears to originate in the Bacteria or Schizomycetes, from which are derived the whole group of Fungi. The second and third do not concern our subject. He considers that "too little importance has at present been attached to degeneration or retrogression, which may be exhibited in the partial or complete suppression of either the reproductive or the vegetative parts." Mr. G. Massee, referring to this subject, says: 3 " The evidence in support of the idea that the fungi are derived from the algae by retrogression, is the close morphological agreement of both vegetative and reproductive parts presented by certain sections of the two groups; for example, in the subdivision of fungi called Phycomycetes the vegetative portion frequently consists of a long, aseptate, variously branched cell or hypha, similar to the vegetative portion of such algal genera as Vaucheria; in the reproductive portion asexually formed ciliated zoospores occur in Pythium, Saprolegnia, Cystopus, etc., while oogonia containing one or more oospheres, fertilised by motile antherozoids, occur in Monoblepharis. In a second group, the Mucorini, the sexual mode of reproduction is effected by the conjugation of two similar branches, as in the Conjugatae, the resulting zygospore becoming invested

¹ See The Dual Lichen Hypothesis, by M. C. Cooke, p. 6.

² Journ. Linn. Soc., "Botany," xxvi. p. 49. 1887.

³ Evolution of Plant Life-Lower Forms, by G. Massee, p. 150. London 1891.

by a thick cell wall, and forming a resting spore. Many species belonging to the *Phycomycetes* are aquatic, being parasitic in the tissues of aquatic plants or animals."

A German author, Dr. Oscar Brefeld, who has accomplished an immense amount of hard work in investigating life-histories, is the authority for the classification of Fungi upon somewhat of this principle. He divides all Fungi into two primary groups-first, the Phycomyceteae, or Algal-like Fungi, characterised by sexual as well as asexual modes of reproduction; second, the Mycomycetes, where the sexual phase is completely arrested, and consequently they are propagated exclusively by asexually formed spores. He further divides the Phycomycetes into Zygomycetes, producing zygospores by conjugation, and Oomycetes, producing oospheres that are fertilised by motile antherozoids, or by transfusion of the contents of passive antheridia. The other group, or Mycomycetes, are also subdivided into Ascomycetes and Basidiomycetes, with the Ustiligineae as a transition group between Phycomycetes and the Basidiomycetal group of the higher Fungi.

Earlier than the above, Sachs proposed a very peculiar arrangement of Thallophytes, which failed to secure general acceptance. In this arrangement Algae and Fungi were terms practically abolished, and the series ran in parallel lines. "The sole character made use of in their primary classification was the mode of reproduction. First came the Protophyta, in which no sexual mode of reproduction is known, followed by three primary classes, the Zygosporeae, Oosporeae, and Carposporeae, distinguished solely by the degree of complexity of the sexual process. Each of these four classes was then divided into a series containing chlorophyll, and a series not containing chlorophyll, the former including the organisms hitherto known as Algae, the latter those known as Fungi."

The views of Brefeld and his coadjutors seem so likely to influence the future of mycologic study, that we may be justified in giving an abstract of them as summarised by Dr. Von Tavel.¹ According to these authorities, Fungi should be classed in two primary groups: (1) the Phycomycetes, consisting typically of a single cell with sexual functions, the nearest

1 Vergleichende Morphologie der Pilze. Jena, 1892.

approach to the Algae; and (2) the Mesomycetes and Mycomycetes, those higher Fungi with a many-celled thallus, destitute of sexual organs.

The Phycomycetes are subdivided into two distinct subsections, which are termed the Oomycetes and the Zygomycetes. In each of these the whole plant consists of a sparingly branched non-septate cell, which reproduces itself sexually by antheridia and oogonia, and asexually by swarm-spores generated The Oomycetes exhibit retrogressions, which are in sporangia. of the nature of adaptations to a more terrestrial mode of life, accompanied by a progressive loss of sexuality. The families of the Oomycetes are-the Monoblepharideae, with antheridia and oogonia in the form of sporangia, and asexual sporangia; and the Peronosporeae and its allies, with the antheridia reduced, the oogonia as sporangia, and asexual sporangia or conidia. These are united to the Zygomycetes by the intermediate family Entomophthoreae, in which both antheridia and oogonia are reduced and conjugate, and there are asexual gonidia. The subsection of Zygomycetes has the sexual fructification in zygospores, and the asexual in sporangia and gonidia. In this subsection there is a still further degeneracy in sexual reproduction. Instead of the union of antheridia and oogonia to produce the zygospore, there is only a conjugation of the beginnings of such sporangia, because the conjugating threads are only slightly swollen, and the male and female organs are not to be distinguished. Asexual sporangia are present, but the spores have lost their cilia, and are more decidedly adapted to a terrestrial life. Five families produce sporophores anywhere on the mycelium, the other two bear their sporophores on specialised threads which arise from the ordinary mycelium.

The second primary group consists of the higher Fungi, in two subsidiary sections: (1) the *Mesomycetes*, which connect the higher Fungi with the Phycomycetes, and (2) the *Mycomycetes*, which include the Ascomycetes and the Basidiomycetes. The sexual organs entirely disappear in these higher Fungi, not being found even in the elementary state, whilst asexual reproduction appears under a multiplicity of forms. The Mesomycetes include two subsidiary groups: (1) the Hemiasci, in which the fructification is by sporangia and gonidia, the

8

sporangia being asci-like; and (2) the Hemibasidia, which connect the basidia-bearing forms with the simpler Zygomycetes. The former of these, the Hemiasci, consist of three families: (1) the Ascoideae; (2) Protomyceteae; and (3) Theleboleae. In these simple forms the sporangium becomes like an ascus, but indeterminate in size or form or the number of spores, and these latter are usually shot out with considerable force. The Hemibasidia fructify by gonidia without sporangia, but the gonidiophores partake of the character of basidia. This group includes the Ustilagineae and the Tilletiae. According to the views of this author all the higher Fungi had their origin in Zygomycetes, and the two series of Basidiomycetes and Ascomycetes were developed in different directions, the former excluding sporangia, and developing specialised gonidiophores or basidia, while the latter retained indefinite gonidiophores, but developed those special sporangia which are known as asci.

This brings us to the Mycomycetes, which, as already stated, consist of two series: (1) the Ascomycetes, where the fructification is by definite sporangia (asci) and conidia; and (2) Basidiomycetes, in which the fructification is by gonidia without sporangia, and the gonidiophores are determinate (basidia). Ascomycetes are characterised by the presence of the ascus, which is a sporangium of determinate form, and the number of its spores. In many cases this form of fructification is accompanied by gonidia and chlamydospores. When mature the spores are often forcibly expelled. Sexual organs do not occur, since the earlier observations ascribing sexuality have been found to consist of misinterpretations. The Ascomycetes are subdivided into Exoasci and Carpoasci. The Exoasei have naked asei borne directly on the mycelium. The Carpoasci have fruit-bodies; the asci are not naked, but are contained in special organs composed of fertile hyphae and sterile threads, which latter form the walls of the envelope. The simplest forms of ascus fruits are angiocarpous, and in the highest of the Pyrenomycetes with a special ostiolum. In the Discomycetes and Hysteriaceae they are gymnocarpous, or closed at first and afterwards open. The Carpoasci have also accessory fruit-forms, and in addition to free gonidia and

chlamydospores there are gonidia which are produced within special fruit-bodies, or perithecia. Another form of fruit is believed to be possible, but has not been found, and these are ordinary sporangia. The simplest form of gonidia in the Taphrineae is developed directly from the ascospore, or from another gonidium. A further advance is the production of a germ tube on which gonidia are borne. From this it is a short transition to mycelium bearing gonidia on its surface. These simple forms may be traced through complex stroma-beds into the highest specialisation of closed fruit-bodies, sometimes called pycnidia. Free gonidiophores and gonidial fruit bear usually but one kind of spores, but sometimes the last produced are of a different shape from the first. Although the ascospore is the highest form of fructification, the Fungus often reproduces itself for generations without developing asci; and hence many gonidia and chlamydospores have been classed as "imperfect Fungi" under Hyphomyceteae, Sphaeropsideae, etc.

The Basidiomycetes are a very large group, and their important character is the possession of basidia, which are sporophores or gonidiophores, restricted in size, shape, and the number of spores. Ordinary gonidiophores produce spores one after the other, indefinitely, but a basidium produces only a definite number of spores, and only once, and in a particular place, and then it shrivels up. Most basidia bear four spores, but some produce two, six, or eight. As a rule basidiospores are borne on long sterigmata. The Basidiomycetes are arranged in two groups: (1) the Protobasidiomycetes, in which the basidia are septate, and (2) the Autobasidiomycetes, in which the basidia are not septate, and bear a definite number of The Protobasidiomycetes, or Fungi with a basidiospores. septate basidium, are ranged in four distinct groups: (1) the Uredineae have horizontally septate basidia, always free, never borne in fruit-bodies, and always produced from a chlamydospore or teleutospore; (2) the Auricularieae have basidia resembling the Uredineae, but gymnocarpous, viz. having fruitbodies which from the beginning form open hymenia; (3) Pilacreae, with horizontally septate basidia, but angiocarpous or closed fruit-bodies; (4) Tremellineae, having vertically divided basidia borne in gymnocarpous fruits.

The Autobasidiomycetes have non-septate basidia, bearing spores only at the apex. They include (1) Dacryomycetes, (2) Gastromycetes, and (3) Hymenomycetes, of which the last is by far the largest. In the first of these the basidia split downwards into two forks, but are not septate. In the second the Gastromycetes have the basidia borne inside various kinds of closed fruit-bodies (peridia), whilst Phalloideae are a subsection, with the basidia in their early stages borne in a closed fruit-body, but afterwards pushed into the air and exposed. In the third, or Hymenomycetes, the basidia are short and simple, bearing normally four spores on delicate sterigmata, but always finally gymnocarpous or semi-angiocarpous. The simplest Hymenomycetes are without a fruit-body. The more complex forms seem to have originated from these. They are followed by the gymnocarpous Thelephoreae and Clavariae. Then come the hemi-angiocarpous forms, with the hymenium on the under surface of the pileus, on the spines of the Hydnei, the walls of the pores in the Polyporei, and on the gill-plates of Agaricineae. Accessory fruit-forms are rare in the Polyporei, but oidia or chains of gonidia occur in some species, while Heterobasidium bears ordinary gonidia, and Oligoporus and Fistulina bear chlamydospores. In the Agaricineae no ordinary gonidia have been found, but oidia occur in certain genera, and especially in Nyctalis, where chlamydospores are also abundant.

This is but a brief summary of the views enunciated by Brefeld and his disciple Von Tavel, which may be further illustrated by the following table :—

I. PHYCOMYCETES

With a One-celled Thallus and Sexual Organs.

1. Monoblepharideae. 2. Peronosporeae. Ancylisteae. Saprolegniaceae.

? Chytridiaceae. 3. Entomophthoreae.

I. OOMYCETES .



II. HIGHER FUNGI

With Septate Thallus and no Sexual Organs.

A. MESOMYCETES

III. HEMIASCI .		∫ I.	Exoh	emias	ci.	1.	{Ascoideae. Protomyceteae.
		(11.	Carp	ohemi	asci	2.	Theleboleae.
IV. HEMIBASIDIA	•	•		•		${1. \\ 2.}$	Ustilagineae. Tilletiae.

B. MYCOMYCETES

V. Ascomycettes	$\int_{a}^{a. Exoasci} \dots $	1. {Endomycetes. Taphrineae. (Gymnoasci.
	b. Carpoasci	2. Perisporiaceae. Pyrenomycetes. 3. Hysteriaceae. Helvellaceae.
VI. BASIDIOMYCETES .	(a. Protobasidiomycetes	$\begin{cases} 1. & { Uredineae.} \\ Auricularieae. \\ 2. & Pilacreae. \\ 3. & Tremellineae. \end{cases}$
T. DASIDIOMYCETES .	b. Autobasidiomycetes	4.Dacryomycetes.5.Gastromycetes.Phalloideae.6.Hymenomycetes.

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CHAPTER XI

NAKED-SPORED FUNGI-BASIDIOMYCETES

THE only safe course in the study of Fungi or any other of the multitudinous organisms, whether animal or vegetable, with which the earth teems, is to proceed step by step from the general to the particular by a systematic sequence. In a few cases it may be possible by a reference to figures, or from incidental circumstances, to attach a name with some approach to accuracy, but such an act is of no service-it teaches nothing, it avails nothing, it is only a sham, a delusion, and a snare. The only road to knowledge is a rough one, but it must be traversed, and all its difficulties surmounted; there can be no creeping upwards by a by-path, for all the bypaths end at a precipice. The most we can do is to tread firmly, walk circumspectly, and look upwards. The study of Fungi is not an easy one, and cannot be got over empirically, but with application and perseverance the difficulties, which seemed at first appalling, become less so at every step.

An effort has been made in the previous chapter to give a general idea of the scope of the subject, but such efforts are never thoroughly effective, cannot be final, and at the best consist only of a shadowy outline. In the present instance this outline has indicated the existence of a great group or cluster of groups in which the spores are produced naked that is to say, not enclosed in a general vesicle or envelope, but borne at the apices of spore-bearing threads. The supports are sometimes highly developed, but in the primary section, the *Basidiomycetes*, they are short and thick comparatively, and as the name indicates, these basidia, or supporters, are the distinctive feature in the section.

The term *Basidiomycetes* is a comparatively new one, and includes the older *Hymenomycetes* and *Gastromycetes*, on account of their agreement in the possession of basidia, although they still remain distinct on account of other differences; but mainly because in the former the hymenium is always naked and exposed, whereas in the latter it is enclosed within a peridium during the early stage, and is only exposed by the rupture of the peridium, when the spores are nearly or wholly mature. It is easy, therefore, to distinguish at a glance the



FIG. 47.—Hymenial cells of Agaric. a, paraphyses; b, basidia; c, cystidia.

true Hymenomycetes from the puffball family or the Gastromycetes, so different are they in external features, and only correlated by a minute character which is not to be demonstrated without the aid of a micro-As Fries was not expert in scope. the use of this instrument, and seldom took into account features which could not be observed with a pocket lens, he appears not to have suspected the presence of basidia in the Gastromycetes, whilst he possessed such a remarkable intuition of the relationships of most of the groups, that he placed these

two orders in juxtaposition. Montagne and Berkeley were the first to indicate the structure of the hymenium in the puff-balls, and demonstrate the presence of basidia.¹

It will facilitate a comprehension of the terms employed in this connection if we indicate the features of the hymenium in *Agaricus*, in its old and broadest sense one of the genera of the *Hymenomycetes*, which may be accepted as the type of the rest. The various modifications of the hymenium in the several families may be reserved for illustration when the *Hymenomycetes* come under special notice. It may be premised that in the Agarics the hymenium or sporebearing surface covers completely the thin membrane, which is pleated and folded on the under side of the cap, and con-

¹ Annals of Nat. Hist., iv. (1840), p. 155.

NAKED-SPORED FUNGI-BASIDIOMYCETES

stitutes what are popularly termed the gills. The whole of this surface is covered with a layer of elongated cells, packed closely side by side, and attached at the base. These hymenial cells are of three kinds intermixed, although regarded by some authors as only variations or modifications of one type (Fig. 47). The most important of these cells are the fertile ones, or those which bear the spores at the apex, and in fact are the true basidia. We may assume it to be generally true that these basidia are more or less of a clavate, or club-shaped, form, narrowed a little at the base into the supporting hypha, and obtuse at the apex, where they are crowned with four delicate. short, spine-like processes-the sterigmata, each of which is ultimately surmounted by a spore. Thus, then, each basidium is normally tetrasporous, producing at its apex four spores. In rare cases there may be only two, but typically there are The cell of the basidium, as indeed all the cells of the four. hymenium in the Agarics, is uncoloured, but the spores may be either colourless or coloured according to the group to which the species belongs. The second kind of cells to be observed on the hymenium are often larger and longer than the basidia, naked at the apex-that is to say, without sterigmata or spores. They also are much fewer in number, and are called cystidia. In some genera these cystidia are very large and conspicuous, and in certain Polyporei and Thelephorei they undergo considerable modification, and are sometimes coloured. At least such are the features of the processes which hold an analogous position to the cystidia, and which are now generally regarded as modified cystidia. As to the functions of these cells opinion is still divided. Some have claimed for them the character and functions of antheridia, but the majority follow De Seynes in regarding them as hypertrophied basidia, and possibly their mechanical function is that of keeping the lamellae apart. The third kind of cells on the hymenium are rather smaller than the basidia, similar in form, rounded at the apex, but without sterigmata, and are sometimes called paraphyses. There can be no doubt that they are abortive basidia or, as De Seynes terms them, "atrophied basidia." So that the three kinds of cells on the hymenium are but three forms or conditions of the same organ-the true basidia, the hyper-

121

trophied basidia, and the atrophied basidia. It is not necessary to discuss the question, when we are occupied rather with the form than the functions of the hymenium. It will, however, be borne in mind that it has of late been the custom of some writers to apply the term "basidia" also to the short sporophores which are present in the Sphaeropsideae and elsewhere, which support the solitary spores. Against such a misappropriation of terms it will be advisable to guard ourselves, and restrict the name of basidia to the spore-supporters in the Basidiomycetes, where they are not simple sporophores in the sense that they support a single spore, but tetrasporous hymenial cells, surmounted by spicular sporophores. The same term cannot, therefore, be equally applied to the appendages of a proper and distinct hymenium and the filiform spore-bearers developed from the base or side walls of a diminutive receptacle. A true hymenium always consists of closely-packed hymenial cells; and we shall find in the Hymenomycetes that not only may it assume the form of gillplates, as in the Agaricini, but also as a lining to porous tubes, as in the Polyporei, be diffused over the surface of teeth or spines, as in the Hydnei, spread over a plane on one side only, as in the Thelephorei, or covering both sides of a vertical hymenophore, as in the Clavariei.

In the other order, the *Gastromycetes*, the basidia closely resemble those of the *Hymenomycetes*, and have the same function, bearing spicules at the apex, usually quaternary, sometimes in pairs, and each surmounted by a spore. The examination must be made in a young state to discover the basidia, because when mature, and the periderm is ruptured, nothing will be observed except a mass of free spores, sometimes with the spicule attached and a number of threads. This is the normal condition in the *Lycoperdaceae*, but varied in the *Phalloideae*, and also in the *Nidulariaceae* and *Hypogeae*. In all it will be recognised at once that the hymenium is less highly developed than in the *Hymenomycetes*, and more fugitive. Paraphyses may be present as abortive basidia, but the cystidia are scarcely distinct.

Berkeley records the results of his examination of a cut section of young Lycoperdon. "If a very thin slice be taken,

NAKED-SPORED FUNGI-BASIDIOMYCETES 123

while the mass is yet firm, and before there is the slightest indication of a change of colour, the outer stratum of the walls of these cavities is found to consist of pellucid obtuse cells, placed parallel to each other like the pile of velvet, exactly as in the hymenium of an Agaric or Boletus, but without any trace of those processes which have been regarded by some authors as male organs (cystidia). Occasionally one or two filaments cross from one wall to the other, and once I have seen these anastomose. At a more advanced stage of growth four little spicules are developed at the tips of the sporophores-all of which, as far as I have been able to observe, are fertile and of equal height-and on each of these spicules a globose spore is seated (Fig. 48). It is clear that we have here a structure identical with that of the true Hymenomycetes, a circumstance which accords well

with the fleshy habit and mode of growth." In his further observations, in reference to the Phalloidei, he says that "the fructifying mass consists of a highly sinuated hymenium. The walls are composed of elongated, somewhat spathulate, cells, surmounted with from four to six spicules, each of which bears an oblong FIG. 48.-Basidspore. The sporophores here again appear to

be all fertile and of nearly the same height. will be observed that when the number exceeds four, the additional spicule is seated between the two, which form one side of a square, and that if a sixth is present it is placed opposite to the fifth. Here again we have an Hymenomycetous fungus, and there can be no doubt that the same structure will be found in all the Phalloidei."

Thus, then, the relationship between Hymenomycetes and Gastromycetes may be regarded as established. But Mr. George Massee, who is nothing if not evolutionist, has some pertinent remarks on this subject in a recent monograph.¹ He observes that in the Hymenomyceteae "the progressive differentiation of the sporophore persistently aims at one object, that of concealing the hymenium until the spores are mature-a statement

¹ Monograph of the British Gastromycetes, by George Massee, p. 2. London, 1889.



ium and spores

of Lycoperdon.

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which is not in harmony with the general conception that the hymenium is from the first exposed. In the Thelephoreae, Clavarieae, and Hydneae the hymenium is exposed from the earliest stage; whereas in the Polyporeae and the Agaricineae the hymenium, in the higher forms, is completely differentiated while yet concealed by a structure known as the veil, which in many species is only ruptured by the expansion of the pileus when the spores are mature. The idea of concealing the hymenium from the light is equally apparent in the various orders enumerated, except in the Clavarieae. In the Thelephoreae the simplest genera-Corticium, Coniophora, and Peniophora-have the hymenium covering the whole of the uppermost or free surface of the hymenophore, and consequently, from the earliest period of development, exposed to the light; whereas in the genera Stereum and Thelephora a portion of the hymenophore becomes free from the substratum and bends over, thus turning the hymenium away from the light; and by a series of transitions we find the higher species of the two last-named genera assuming umbrella-shaped forms with a central stem and inferior hymenium, but not at any period covered by a veil. In the Agaricineae we meet with the same sequence of the evolution. In such low forms as Cantharellus retirugis and Agaricus (Pleurotus) hypnophilus the plants are fixed to the substratum by the pileus with the hymenium uppermost, and may be compared to a Corticium, with the hymenium imperfectly broken up into gills; whereas in such species as Agaricus (Pholiota) praecox and Agaricus (Amanita) muscarius the hymenophore is supported on a stem with the hymenium on the under side, and concealed by a veil until the spores are mature." It might also have been urged here, in confirmation, that specimens of Fomes and Polystictus from tropical or sub-tropical regions, where the light is strong, are constantly to be met with, in which the log has become turned and the hymenium of the Polypores growing thereon exposed to the full light. In such cases, and especially in such common species as Polystictus sanguineus and Polystictus occidentalis, the old hymenium gradually becomes obliterated, and a new hymenium is formed upon what previously was the upper surface, but accidentally inverted so as to

NAKED-SPORED FUNGI-BASIDIOMYCETES 125

become the under, and consequently turned away from the light.

"In the Gastromycetes, with the exception of the species constituting the genus *Gautiera*, the hymenium is completely concealed by a continuous wall or peridium, until the spores are mature. . . As already stated, two leading features stand out prominent in the evolution of the *Hymenomycetes*: the conversion of the primitive even hymenial surface into gills, thereby increasing the spore-bearing area, and secondly, the gradual concealment of the hymenium until the spores are mature. In the Gastromycetes these two conditions are present in the lowest forms, and persist throughout the group, the very varied forms presented by the different orders being the outcome of modifications of the sporophore in connection with spore dissemination."

We may now proceed to a closer analysis of the two separate orders of *Hymenomycetes* and *Gastromycetes*.

CHAPTER XII

HYMENOMYCETES

As lately as 1830 the Botanicon Gallicum included under the term "Fungi" only the Hymenomycetes and the Discomycetes; whilst at a much later period the ordinary observer recognised only a few forms, chiefly of the Discomycetes, as Fungi beyond the Hymenomycetes. The puff-balls came at length to be included, but even these for a long time were regarded doubtfully as to whether they were true Fungi or not. In this country it was not until 1836, when Berkeley's volume of Hooker's English Flora was published, that the proper limits of "Fungi," as then known, came to be under-Under any circumstances the Hymenomycetes have held stood. the first place amongst Fungi, are usually the first to attract the attention of students, and stand at the head of every list, catalogue, or "Fungus flora." In 1825 Elias Fries himself included Discomycetes within his order "Hymenomycetes," and did not practically dissociate them until 1849, when he constituted the Discomycetes as a distinct and separate order. At that period the two orders followed each other, whilst the Gastromycetes were at a distance and scarcely became approximate until the basidia had been discovered in them.

The limits of the order Hymenomycetes were thus briefly expressed: "Spores naked. Hymenium free, mostly naked, or if enclosed at first, soon exposed." This again was more expanded and rendered clearer by Berkeley, thus: "Mycelium floccose, giving rise at once to a distinct hymenium or producing a variously shaped naked or volvate receptacle, even or bearing on its upper or under surface various folds, plates, prickles, etc., clothed with fertile hymenial cells." The pre-

HYMENOMYCETES

ceding chapter having prepared us for the general attributes of the order, we may proceed to indicate the six groups into which the genera naturally fall. Four of these have the hymenium normally inferior, in the other two either superior or on all sides. The four first are the *Agaricini*, *Polyporei*, *Hydnei*, *Thelephorei*, and the two latter *Clavariei* and *Tremellini*.

The *Agaricini* are pre-eminently soft, fleshy, putrescent Fungi, of the mushroom type, in which the inferior hymenium, or spore-bearing surface, is spread over folds, or gills, which



FIG. 49.—Agaric. A, young state ; B, mature ; C, section.

radiate from a central stem to the circumference of a pileus or cap. In the typical form there is a floccose mycelium of delicate threads, surmounted by a stem, more or less developed, and crowned by a hood or cap of umbrella-like form, with gills on the under surface. In the earliest condition the form is nearly globose, enclosed like an egg within a thin shell or membrane. As it progresses in growth the egg-shaped body splits round the centre, the upper hemispherical portion being carried upwards by a quick-growing stem, forming the cap, the lower half remaining behind to constitute the base. At the margin of the pileus the jagged remains of the fissured membrane often adhere for some time, and in like manner there
may be traces of the fissure on the basal portion. In the most highly developed forms patches of the broken envelope, or volva, adhere like warts to the top of the pileus, whilst the basal portion remains as a loose sheath at the bottom of the stem, where it is for some time persistent as a kind of sheath, called the volva. By cutting through the entire Fungus longitudinally from the apex to the base, the cut section exhibits the following features-a rooting mycelium, or spawn; an erect stem rising therefrom (s), which is sometimes solid and sometimes hollow (Fig. 49); the base either equal in dimensions or swollen like a bulb, occasionally with a distinct outer coat or volva (v), which is adnate below to the bulb and free above; the stem is surmounted by a more or less hemispherical or conical cap or pileus (p), the under surface covered with parallel plates, or gills, which radiate from the stem to the margin of the cap (g). When the cap is hemispherical the gills are often covered at first by a thin membrane, which extends from the stem to the edge of the cap; and, as growth and expansion proceed, this veil is torn away from the margin of the pileus, and hangs like a collar or frill around the upper part of the stem, forming an annulus or ring (a). When the cap is conical the edges of the gills are closely applied to the stem vertically, and the edge of the cap is only slightly attached to the stem, not forming a When the substance of the cap descends between the ring. folds of the gills it is the trama, and then the gills do not part freely from the cap; but when the trama is thin or obsolete, the gills part freely from the flesh of the pileus. The gills are formed by a membrane, which constitutes the hymenium, and is folded like a fan; so that each gill is a double membrane, applied back to back, giving as much surface as is possible for the production of the spores. The appendages of the hymenium have already been described as basidia, cystidia, and paraphyses, with the resulting tetraspores. Thus much may be seen of the structure in a longitudinal section of the pileus and stem. Modifications in some one or more of these general details give rise to the different genera into which the Agaricini are now divided. In former times, when the system adopted by Fries absolutely prevailed, the greater part of the species of Agaricini were comprised in one large genus, that of

Agaricus, in which the gills were membranaceous, and persistent, -that is to say, not melting or deliquescent when mature; the trama was continuous with the substance of the pileus, passing down between the folds of the hymenium, and the edge of the gills was acute. The substance was fleshy and putrescent, not reviving after being dried. In other genera, as in Coprinus and Bolbitius, the gills deliquesced when mature. In such genera as Panus, Lentinus, and Lenzites the substance was not fleshy but somewhat leathery, and not putrescent. In the large genus Marasmius, as well as in Xerotus and Trogia, the substance was thin but dry, not putrescent; readily desiccated, and reviving when moistened. In Russula the substance was fleshy and putrescent, but there were peculiar and special features which severed it from Agaricus, approaching Lactarius, in which latter a peculiar milky secretion afforded a distinctive feature. Hygrophorus and Cortinarius were two other rather large genera with distinctive characters, to be alluded to hereafter. Cantharellus and Schizophyllum afforded prominent characters in their thickened or splitting gills. Hence it will be seen that the old genus Agaricus had one or two prominent characters, which distinguished it from all the other genera of the Agaricini, and held together one of the largest genera of Fungi, which at the present time would not number less than 3000 species. For the purposes of classification Fries subdivided this genus into five groups, according to the colour of the spores-the Leucosporae, in which the spores were typically white or but slightly coloured; the Hyporhodii, in which the spores were pink or salmon-coloured; the Dermini, in which the spores were tawny or some shade of rusty brown; the Pratellae, in which the spores were brownish purple or very dark brown; and the Coprinarii, in which the spores were black. These divisions are substantially maintained in more recent times, but applied to the whole of the Agaricini.

In the Friesian system each of these groups was subdivided into subgenera, which had their analogues in part in the kindred groups. In a *Clavis* published by Mr. Worthington Smith he indicated the corresponding subgenera in each of the five sections, as far as they were represented in the British flora. All this disappeared when Professor Saccardo

129

9

propounded his scheme for the classification of the Agaricini, for which previous authors had prepared the way, by at once elevating the subgenera of Fries to the rank of genera, and ranking them upon an equality with the other old Friesian genera. This was the inherent weakness of the Saccardian arrangement, although it will doubtless come into universal use where expedients are valued rather for their utility than their consistency. No one of experience would contend that *Tricholoma* and *Collybia* bear absolutely the same relation to each other that *Tricholoma* would bear to *Cantharellus*, or *Collybia* to *Lentinus*.

In the Saccardian system the four primary groups into which the whole of the Agaricini are divided, depend upon the colour of the spores. The Leucosporae, having the spores colourless or but faintly coloured; the Rhodosporae, in which the spores are pink or salmon-coloured, corresponding absolutely to the Hyporhodii of Fries; the Ochrosporae, in which the spores are ochraceous, tawny, or some tint of light brown; and the Melanosporae, in which the spores appear to be black but in reality are dark brown, purple brown, or black, and thus combining the attributes of the Pratellae with the Coprinarii of Fries. Of all these groups the first and largest is the Leucosporae, containing upwards of 3000 species, or more than half of the whole Agaricineae, which numbers about 5245 species. These are represented by thirty-two genera, and these latter arrange themselves in two groups or subdivisions-the larger, or Haplophyllae, with the edge of the gills entire, and the Schizophyllae, in which the edge of the gills is split or appendiculate. The latter is a very small series, consisting of four genera but numbering in all not more than fifteen species. Hence, then, the Haplophyllae are the only series which require any special notice in this place; and these are subdivided once more into two subsections, in which the chief distinction consists of the texture of the substance. In the first, or Molles, the substance is more or less fleshy, and putrescent, not reviving after desiccation. In the second, or Tenaces, the substance is tough and persistent, reviving after being dried. These are useful distinctions to be borne in mind, and will soon commend themselves to the practical Fungus-hunter. The

common mushroom may be taken as an illustration of the former, and some species of Marasmius or Lentinus of the latter.

This brings us in face of the fleshy, or Molles, section of white-spored Agarics, containing in 1893 about 1750 species, of which not more than 430 are British, having the edge of the gills acute and the folds of the hymenium separable. This corresponds therefore with the Leucosporae section of the old genus Agaricus. Nevertheless there are additional genera which agree in their fleshy substance but differ in other particulars. In this category Hygrophorus is a genus by itself, with the gills continuous with the pileus, and not separable Thus the gills and the pileus are practically from the trama. of one piece. Many, and indeed most of them, are more or less glutinous when fresh, and perhaps for this reason are capable of enduring more frost than others of the fleshy Agarics. In addition to these are two genera which have the substance of the pileus of a peculiar vesicular character, soft and fragile, but which have also another remarkable feature of affinity with each other in the spores being normally globose. These

two genera are Russula and Lactarius, the latter with and the former without a milky juice (Fig. 50). In habit and appearance they most resemble Tricholoma, but a little experience will soon distinguish the difference. They are almost absolutely terrestrial and solitary, with a short robust stem, and many of the Russulae have a brightly coloured pileus. Commonly, but not universally, the gills in Russula reach from the margin to the stem without FIG. 50. -Lactarius deliciosus, intervening short gills; or, when



with section and spores.

shorter gills are present, these usually anastomose with the long gills, so as to appear as if the latter were forked. Finally there is a small group-consisting of four genera, of which Cantharellus is the chief-in which the edge of the gills is obtuse or vein-like. All these subsidiary groups together contain about 500 species, bringing the total of fleshy, white-

spored Agarics of all kinds up to 2250 species, or nearly one half of the whole gill-bearing *Hymenomycetes*.

The other section of the Haplophyllae, with a tough persistent substance, includes six genera in which the substance is at first fleshy, or gelatinous, and then becoming leathery, and three genera in which the substance is always more or less corky or woody. As might be anticipated, these are almost the only representatives of the gill-bearing Hymenomycetes which extend into tropical countries. Of the six genera first alluded to, Marasmius approaches nearest to the soft-fleshed Agarics, such as Collybia and Mycena, and might readily be confounded, save for their tougher and drier substance. The larger proportion are of a small size, and these affect dead wood and leaves. Lentinus often attains a large size, and, with the exception of a few European species, is a tropical or subtropical genus. The technical distinction between Panus and Lentinus is that in the former the edge of the gills is even, and in the latter toothed or ragged. In order to complete our numerical estimate, we may add that the Tenaces section of Haplophyllae is represented by about 810 species. The next order of Hymenomycetes, the Polyporeae, is approached most nearly in one direction by Lenzites, which is the analogue in the Agaricineae of Daedalea in the Polyporeae.

It seems unnecessary in this place to descend any lower with an analysis of the *Leucosporae*. The analytical key to the genera in any good local flora will indicate the salient features in each genus, which it would be rather tedious to introduce into a book having the character of a general introduction, and would moreover extend this chapter to an inordinate length.

We must now revert to Saccardo's second primary group of the *Agaricineae*—that of the *Rhodosporae*, so called on account of the spores being pink or of a salmon colour. It may at the same time be intimated that, although in some instances these spores are elliptical and smooth, they are often coarsely warted and angular. The group in itself seems to be a very natural one, for the species are all soft and fleshy, and even more putrescent than the softer of the *Leucosporae*. In all countries they constitute the smallest of the four primary groups of the *Agaricineae*, and have often a disagreeable odour. The total

number of known species does not exceed 366, or about oneeighth of the number of white-spored species. There are no genera, recognised as such, in the Sylloge, except such as were included by Fries as subgenera in his genus Agaricus, and these correspond to analogous genera in the Leucosporae. For instance, the recent genus Metraria corresponds to Amanita. and Volvaria to Amanitopsis; Annularia is an analogue of Lepiota, as Pluteus is of Schulzeria, but there is no correspondent to Armillaria. Entoloma is analogous to Tricholoma, Clitopilus to Clitocybe, Claudopus to Pleurotus, Leptonia to Collybia, Nolanea to Mycena, and Eccilia to Omphalia. In this way the characteristic features of the genera which have been learned in connection with the Leucosporae may serve again with the Rhodosporae, conditional upon the difference in the colour of the spores. It is somewhat remarkable that the genus Metraria is only known from Australia, and yet there are known at present only twenty-five other species of the Rhodosporae in that large continent, which are spread over ten. genera, and fifteen of the species are European. In the British flora upwards of 100 species are recorded, or about one to seven of the Leucosporae. In Australia the proportion is one to thirteen and a half of the Leucosporae. This indicates that the Rhodosporae prefer a cold to a warm climate, or at least a moist to a dry one. In Ceylon the proportion is much the same as it is in Britain.

The third primary group is Ochrosporae, which includes the Dermini section of Agaricus, with the addition of the large genus Cortinarius, and the small genus Paxillus—to which, we contend, should also be added Bolbitius, placed by Saccardo in Melanosporae, but evidently the colour of the spores is against this position. The genus Paxillus is distinct from all the rest in the facility with which the gills separate from the hymenophore; and Cortinarius differs from all in the universal veil being of delicate threads like a spider's web. The residue are the same as the Friesian subgenera of the section Dermini. Exception might be taken to the term Ochrosporae, as not being characteristic of the general colour of the spores, which are much too deep for "ochraceous," approximating more to ferruginous, and hence the name is misleading. As we have

done with the Rhodosporae, so we might indicate the analogues of the Leucosporae in the Ochrosporae, in so far as they are represented. There is no genus which corresponds with Amanita, but Locellina or Acetabularia, whichever name we select, is equivalent to Amanitopsis. Lepiota and Schulzeria have no analogue, but Armillaria has a correspondent in Pholiota. Tricholoma is most nearly represented by Hebeloma. and in some degree by Inocybe, the essential difference between these two genera being the fibrillose cuticle in the latter, and the smooth viscid cuticle in the former, both of which are represented in subsections of Tricholoma. Clitocybe is represented by Flammula in some of its species only, which have decurrent gills, whilst Pleurotus has its analogue in Crepidotus. For Collybia we have Naucoria; for Mycena there is Galera; and Omphalia is recognised in Tubaria. It is only in Inocybe that we meet with irregular spores such as are not uncommon in the Rhodosporae.

The total number of recorded species is estimated at 1157, as against 366 of the *Rhodosporae*. The large genus *Cortinarius* comprises some 400 species, all of which are terrestrial, and only subtropical at considerable elevations. Should *Bolbitius* be included, it differs from all the rest in the thin membranaceous pileus, in which respect it is analogous to *Hiatula* in the *Leucosporae*, and to some species of *Coprinus* in the *Melanosporae*.

The fourth and last primary division of the Agaricineae, according to Saccardo, is Melanosporae, in which he combines the Pratellae of Fries with the Coprinarii, and adds thereto the genera Coprinus, Bolbitius (ochrosporous), Gomphidius, Anthracophyllum, and Montagnites. In some cases it is difficult to distinguish dark purple-brown spores from black, but this is hardly sufficient reason for combining them. Mr. G. Massee felt this to be the case, and in his British Fungus Flora he adopts two divisions instead of one, namely, the Porphyrosporae and the Melanosporae. After all there is no great principle at stake, although personally we would rather, if a coalition be considered advisable, that the two subdivisions were kept separate as Porphyrosporae and Melanosporae under a common designation. Following the same course that we have adopted

in the other primary divisions, we would intimate the analogies of the several genera of the Porphyrosporae. The representatives of Amanita and Amanitopsis must be sought in a single volvate genus-that of Chitonia, in which one or two species are annulate, whilst the residue are not. Lepiota has its analogue in Agaricus proper, which includes the old subgenus Psalliota of Fries, and Schubzeria has its correspondent in the ringless Pilosace. As for Armillaria, we shall find an analogue in Stropharia; and Tricholoma will have its nearest representative, but not a very perfect one, in Hypholoma. Up to the present no purple-spored species with decurrent gills has been found to occupy the place of Clitocybe, which is so largely represented in the Leucosporae, and Pleurotus has also no As for the rest, we have Collybia replaced by analogue. Psilocybe, Mycena by Psathyra, and Omphalia by Deconica. But the same process cannot be applied to the veritable blackspored species, unless we include the deliquescent Coprinus, and can, by a little stretch of fancy, find in the pseudo-volvate species some approach to Amanita, in Anellaria a suggestion of Lepiota, in Panaeolus a suggestion of Collybia, and in Psathyrella of Mycena. At the best these are little more than fanciful analogies. The combined brown and black-spored species do not exceed a total of 630 species.

It will be observed that throughout the whole of this long series of about 5200 species we have but one type, with all its modifications, of a pileate Fungus, with a stem, sometimes nearly obsolete, supporting a cap or pileus, bearing on its inferior surface the radiating folds of a hymenium, on which the basidia support four naked spores. All the groups, divisions, subdivisions, genera, and species are dependent upon the variations in this common type. There need, therefore, be no surprise that a cultivated eye and experience are essential for the accurate discrimination of distinctions, often so subtle as to puzzle the young student and bewilder the casual observer, whose knowledge has never extended beyond a soft fleshy thing with a stem supporting a cap with parallel radiating gills.

The second group of the *Hymenomycetes* is the *Polyporei*, in which the hymenium is still inferior, but is no longer repre-

sented by a folded membrane, in the form of parallel plates or gills. Instead thereof the gills are replaced by parallel tubes, more or less adnate to each other, presenting a surface punctured with an infinity of minute pores, sometimes as small as if pricked with a pin. The membrane which lines the sides of these tubes or pores is the hymenium, so that the spores are produced within the tubes and not so fully exposed as in the *Agaricineae*. If we take as a type one of the species of the soft and fleshy genus *Boletus*, we shall see that in some respects it resembles the ordinary mushroom, and at the same time detect its more prominent differences (Fig. 51). In the presence of mycelium, stem, and cap the *Boletus* agrees with the Agarics, but the section will show the parallel tubes replacing the gills.



FIG. 51.—Boletus, with section and spores.

But this is not so complete a type of the whole *Polyporei* as was the Agaric of the *Agaricini*. In the first place the stem is often absent and the cap or pileus sessile, attached by the margin. And, in the second place, the pileus, or what corresponds to the pileus, adheres to the matrix by its whole upper surface, and only the hymenium, or pore-bearing surface, is exposed. This resupinate condition is very common, so that the essential character is a porous hymenium, seated

upon the least possible development of a pileus. And yet, as far as practicable, the hymenium is inferior, or turned away from the light. We are prepared, then, to meet with a greater variety of form than in the *Agaricini*, as well as greater extremes of texture.

The nearest approach to *Agaricini* in habit is to be found in the four genera *Boletus*, *Strobilomyces*, *Boletinus*, and *Gyrodon*. All these were, in their earlier history, associated together as *Boletus*, but at length came to be dissevered and recognised as distinct genera. *Strobilomyces* is *Boletus* with a scaly pileus; *Boletinus* is *Boletus* with short, large, radiating pores; and *Gyrodon* is *Boletus* with elongated, sinuate, irregular pores. All of these are fleshy but firm, soon putrescent, but mostly

with the tubes of the hymenium adhering so slightly to the under side of the cap that they are easily removed. Otherwise expressed, the trama of the pileus does not descend into the tubes, the mouths of which constitute the pores. In all of these a stem is invariably present, and sometimes a manifest ring, but without a volva. They are usually of a robust habit, sometimes attain a very large size, and are wholly terrestrial. Like the fleshy *Agaricini*, they are most prolific in temperate regions, being replaced in the tropics by woody *Fomes* or leathery *Polysticti*, as fleshy Agarics are replaced by *Lentinus* and *Lenzites*. The whole total of described species is somewhat under 300.

Fistulina has a similar fleshy substance, but the stem may be present or absent, and the tubes are not laterally adherent, and nearly all the species grow upon decayed wood.

The genus *Polyporus*, as originally characterised by Fries, was a large one and spread all over the world, but in recent times it has shared the fate of other large genera, and been subdivided into the genera *Polyporus*, *Fomes*, *Polystictus*, and *Poria*, as suggested by Fries in one of his latest works. These appear to be well defined, and no difficulty will be found to occur practically in their discrimination. The original name is retained for the section *Anodermei* of the old, undivided genus.

The pileus is at first soft and fleshy but tough, becoming indurated, rarely fragile, without furrows or zones on the pileus, and with only a single stratum of tubes, so that practically they are not perennial. Some of the species have a central stem, and then resemble Boletus, only that the trama of the pileus is continuous with the tubes, which are not easily separable from the flesh of the cap. Other species have a lateral stem, or even a common stem, much divided above, and bearing several pilei (Fig. 52). Finally, other species have no stem at all, and the pileus is broadly attached to the matrix, so as to be semi-orbicular or kidney-shaped. Rarely the pileus is reduced to a thin stratum, adherent by its whole surface, as in Poria, but with a slightly reflexed margin. In Fomes the substance is woody from the first, becoming very hard, and covered with a rigid crust; not truly zoned, but becoming concentrically sulcate. The substance is floccose and interwoven,

often zoned, and the tubes are typically stratose, each stratum being the growth of a year, so that the species are truly perennial. Some have a central, others a lateral stem, but most



FIG. 52.—Polyporus, with common stem.

commonly they are attached by a broad base, where they are very thick, and not uncommonly of the shape of a horse's hoof, or more rarely several pilei grow together in an imbricate manner. The species of *Polyporus*, as now restricted, generally shrink and become contorted in the process of drying; but in *Fomes* the substance is so rigid that no shrinking or alteration of form takes place, and, except for the depredation of insects, might be preserved unaltered for a century. Such species as *Fomes*

cornubovis, when sawn through, resemble sections of buffalohorn, although generally the internal substance is more fibrous.

Polystictus includes thinner, smaller, and more delicate species, which are of a somewhat tough and leathery consistency, usually flexible, and either hairy or velvety, or becoming The surface of the pileus may be concentrically smooth. sulcate, normally zoned, but not encrusted. The intermediate stratum is fibrillose, passing down into the hymenophore, so that the tubes are not separable. The latter are short, and developed from the centre towards the circumference. Commonly the whole thickness behind does not exceed a quarter of an inch, often less, sometimes more; but the pilei may be confluent laterally, or densely imbricated, and the hymenium may run down the matrix for a considerable dis-The habit and appearance often closely resemble tance. species of Stereum. Additional to the sessile species, there are some which have a central stem, others with a very short lateral stem, expanded at the base into a sort of disc, for attachment to the matrix; but most of the European species are sessile, extended at the base, and more or less imbricate. The pores are very variable in size in different species; in some they are so small as scarcely to be visible to the naked eye,

in others they may be broad and shallow. The walls or dissepiments are normally thin, even so thin as to split downwards very readily in process of growth, leaving little appearance of pores, except at the base. In some species the edges of the pores are fringed and toothed, so as to resemble *Irpex*.

The last group of those which constituted the old genus *Polyporus*, contains the resupinate species, under the name of *Poria*. The pileus is reduced to a thin stratum, mostly spread over, and adhering closely to the matrix, the outer surface covered with the crowded pores. In habit the resemblance is to *Corticium*, but instead of a smooth horizontal hymenium it is a porous one. Normally the pores are in a single series, whilst in resupinate forms, or species, of *Fomes* they are thicker, firmer, and stratose.

Allied to *Fomes* rather than to *Polystictus*, the genus *Trametes* is to be recognised chiefly by the thick obtuse

dissepiments of the pores, the tubes deeply sunk into the substance of the pileus, and not stratose, and without the hardened crust to the pileus. The pores are rounded and often unequal, whereas in *Sclerodepsis* they are large, sometimes angular, with the edge acute or toothed. Daedalea is in substance and general appearance very like Trametes, with the pores sinuous or labyrinthiform (Fig. 53). Hexagonia rather approaches Polystictus than



FIG. 53.—Daedalea quercina.

Trametes, but the pores are mostly large and hexagonal, with firm entire dissepiments. Favolus differs from Hexagonia in the pores being less hexagonal, but angular and radiating from the stem; most species being substipitate, and fleshy rather than rigid. In Laschia the substance is still softer, and more gelatinous, whilst the dissepiments are vein-like,

and the pores shallower and irregular. The latter genus leads to Merulius, with its soft, waxy hymenium, the surface of which is reticulated with obtuse folds, forming irregular areolae, the folds sometimes rather toothed. This is possibly the lowest and most imperfect of the Polyporei. A recent genus, Campbellia, is a higher development, with a pileus and stem and more distinct pits or pores. Porothelium has the habit of Poria, but the tubes are more scattered, reduced to papillae, and at length pierced and open. Some authors add Solenia to the Polyporei, whilst others have associated it with Cyphella in the Thelephorei.

The third primary group of the Hymenomyceteae is the Hydnei, in which the gills of the Agaricineae and the tubes of the *Polyporei* are replaced by teeth or spines, the outer surface of which is clothed with the hymenium, which is therefore wholly exposed. There is at no time, and in no known species, any kind of veil covering the hymenium in its early stage. The most typical genus is Hydnum, which remains much the same as Fries left it, although there has been more than one proposal to split it up into smaller genera (Fig. 54). In the stipitate species some have a central stem, others a lateral stem, and in

others the common stem is branched and subdivided, but the pilei are imperfect. In another section there is no stem, but the pileus is sessile or imbricate, and there are a large number of species which are as entirely resupinate as in the porous genus Poria, to which this section is analogous. FIG. 54 .- Section of Hydnum repandum. also considerable There is



difference in texture, some being fleshy, others waxy or leathery, and others becoming quite hard and corky. At one time a gelatinous species was included, but this has been removed on account of its affinity in fructification with The teeth are variable in length and thickness in Tremella. different species, but they agree in being more or less pointed at the apex, and free from each other at the base.

A number of small genera are associated together in this family, the modifications consisting chiefly in the teeth or spines; for instance, in *Irpex* the teeth are flattened at the base, and connected so as to form irregular pits; and in *Radulum* the

teeth more resemble obtuse tubercles, and are often distorted (Fig. 55). In *Phlebia*, an aberrant genus, the hymenium is corrugated, with fold-like crests, so as to resemble *Auricularia* almost as much as anything else, and *Hydnum* scarcely at all. Then in the wholly resupinate genera, *Grandinia* has the hymenium granular, *Odontia* has the granules or warts crested, and in *Kneifia* the hymenium is clad with rigid setae. Except in *Mucronella*,



FIG. 55.-Radulum.

and probably *Kneiffia*, the basidia are tetrasporous. The whole family does not include more than about 470 species.

The last of the four primary families of Hymenomyceteae which have an inferior hymenium, is the Thelephoreae, which nearly corresponds to the section Auricularini of Fries, with the exception of the genus Auricularia, transferred to Tremellineae. The hymenium is typically even, but rarely rugose, approaching the Hydneaceae by such genera as Cladoderris and Beccariella, in which the hymenium is veined, and the veins are warted or almost aculeate. Mr. G. Massee has intimated ¹ that " the Thelephoreae constitute the base, and also the starting-point, in the evolution of the Hymenomycetes, and, further, that from the Thelephoreae all the other orders have directly originated."

In this family, as in the others, the species are variable in form as well as in texture. Only in *Craterellus* is the substance fleshy, attenuated in some species to membranaceous, often with a central stem and a funnel-shaped pileus, the outer or under surface being clothed with a ribbed or rugose hymenium (Fig. 56). *Cladoderris* and *Beccariella* are tough and leathery, mostly fanshaped, sometimes funnel-shaped, but with a warted hymenium. In *Thelephora* the substance is tough, but softer and more

¹ "Monograph of the Thelephoreae," by G. Massee, in *Linnean Journal*, xxv. p. 112.

spongy, without distinct cuticle to the pileus, or an intermediate stratum; hence homogeneous, the hymenium being even or a



FIG. 56.—*Oraterellus cornu*copioides.

little ribbed. The form is variable, from stipitate and funnel-shaped to closely adnate and resupinate. It is notable that in the majority of species the spores are globose and rough, mostly slightly coloured. We are disposed to place here the genus *Lachnocladium*, which some authors include in the *Clavarieae*, on account of the erect, branched habit, resembling some species of *Clavaria*, forgetting that there are also erect, branching species of *Thelephora*, to which these species of *Lachno-*

cladium are closely allied in texture rather than to fleshy Clavariae. Stereum in form approaches Thelephora, but the substance is firmer, more leathery, and the pileus has a distinct

outer stratum analogous to that in an intermediate Polystictus, with stratum, and a smooth, even hymenium Closely resembling in (Fig. 57). appearance is Hymenochaete, with the exception that the hymenium is velvety, with processes resembling bristles. With the exception of Skepperia, in which the pileus is vertical, most of the remaining genera are These are : Coniowholly resupinate. phora, in which the effused substance



FIG. 57.-Stereum hirsutum.

is membranaceous and smooth, with coloured spores; Corticium, in which the effused substance is usually thicker and firmer, but without an intermediate stratum, the hymenium smooth and rather waxy, and the spores uncoloured; Peniophora, with the habit of Corticium, but with a velvety hymenium; and Hypochnus, with the habit and appearance of Corticium, but with the substance softer, floccose, and more lax, and the hymenium less compact, but still the spores are uncoloured. To these must be added the small genera—Aleurodiscus, with a somewhat saucer-shaped

pileus, and peculiarities of structure which prohibit its unison with *Corticium*; *Michenera*, with a placentiform habit, a waxy hymenium, and pedicellate spores; and *Exobasidium* and *Helicobasidium*, which are encrusting and waxy, growing upon living plants, and distorting them. Finally, *Cyphella*, having the form of *Peziza* but the fruit of *Corticium*, being in fact a cup-shaped *Corticium*; and *Solenia*, the cups of which are elongated into tubes, so that it seems doubtful whether they should be placed in relationship with *Poria*, in *Polyporeae*, or with *Cyphella* in *Thelephoreae*.

Briefly and succinctly, these are the principal genera of *Thelephoreae*, but before dismissing them we must advert to certain appendages of the hymenium which

distinguish some of the genera above enumerated. In addition to the basidia there are to be found in the genus *Peniophora* stout projecting cells, which are either the modified cystidia, or analogues of cystidia, but which have been called *metuloids*. They are fusiform, colourless, and at first smooth, but afterwards rough and brittle from the deposit of oxalate of lime on



FIG. 58.—Cystidia of Peniophora.

These are conspicuous objects upon the otherwise their surface. smooth hymenium, giving it a velvety appearance, and by this character separating the species from Corticium. In another genus, that of Hymenochaete, the same place and position on the hymenium is occupied by projecting, acute, nonseptate brown bristles, which spring from the hyphae of the subiculum, and impart also a velvety appearance. Externally in habit the species resemble Stereum, but they are readily distinguished by the presence of these brown projecting bristles. A similar kind of appendage to the hymenium has been detected in some species of the Polyporei, for which the generic distinction of Mucronoporus has been proposed. In a small section of the genus Hymenochaete, according to Saccardo, but generically separated by Cooke and by Massee under the name of Veluticeps, the hairs of the hymenium are produced generally in bundles, and are flexuous and septate, in which respect they differ from the setae of Hymenochaete.

143

A type of structure in the hyphae of the basal stratum in some species of Corticium is worthy of note, as affording a means of discrimination in allied forms; and this constitutes the basis of a new genus, proposed by Massee, under the name of Asterostoma. The species alluded to are distinguished by the brown stellate hyphae that are present in the subiculum. "Erect branches at about the level of the base of the basidia develop at the apex a stellate arrangement of branchlets, all situated in one plane, parallel to the surface of the hymenium; the number of rays varies from three to seven, five being the most frequent, and differ from the supporting hyphae in being aseptate, with very thick walls, which soon become bright brown. When the spores are ripe, the erect hyphae, supporting both stellate threads and basidia, along with the latter disappear, leaving the coloured star-shaped bodies mixed with the spores, resting on the horizontal interwoven basal stratum of the plant." An analogous differentiation is pointed out as existing in the basal stratum of Bovista, in the Gastromycetes.

Thus, then, we close our remarks on the first four primary sections or families of the Hymenomycetes, in which the hymenium is normally inferior, and either spread over radiating gills, lining the cavities of tubes, investing teeth, warts, or projections, or finally forming a plane, even, or nearly even, fructifying surface.

The fifth family, or *Clavarieae*, has a vertical hymenophore, with the hymenium on all sides, and not distinct from the stem. Sometimes the entire Fungus is a simple club, and at other times it is much branched, with the lower portion barren, forming the stem, and the upper portion fertile, covered with the even or wrinkled hymenium. In most genera the substance is either fleshy or waxy, rarely somewhat gelatinous. The most highly developed genus is *Sparassis*, in which the branched hymenophore has the branches flattened into leaf-like expansions. The largest genus, however, is *Clavaria* (Fig. 59), in which the hymenophore is club-shaped and simple, sometimes solitary and sometimes in clusters or branched, often very much branched, but always fleshy. In *Calocera* the form is similar, but the substance is toughly gelatinous, becoming horny when dry. The species of *Clavaria* are for the most part terrestrial, those of

Calocera usually growing on dead wood. Saccardo includes also Lachnocladium, which resembles a branched Clavaria, but the

substance is coriaceous, and the stem tomentose. For these and other reasons we prefer to place it in Thelephoreae. In Pterula the substance is dry and cartilaginous, but in form resembling very slender Clavariae. Typhula and Pistillaria include minute species, mostly waxy and delicate, in the former with a very long, and in the latter a very short stem. Physalacria is Pistillaria with a subglobose, vesicular head or capitulum. Most of the species in this group are white, whitish, or brightly coloured, and but few of them attain any considerable size. The spores are simple, small, and either uncoloured or yellowish.

The sixth, and last, family is the *Tremellineae*, in which the distinguishing feature is the tremelloid substance, collapsing when dry and reviving with moisture, combined with a peripherical, somewhat peculiar,



FIG. 59.—Clavaria pistillaris.

basidiosporous fructification. The basidia are not superficial, but immersed, and either undivided or forked at the apex, or globulose and cruciately divided. The spores are typically reniform or globose and continuous, and these on germination give rise to sporidiola. The structure of this family was investigated at first by Tulasne, but more recently by Brefeld, and the classification now adopted is based chiefly upon the records of the latter. In this manner three subfamilies have been recognised — viz. the *Auricularieae*, in which the basidia are elongated or fusoid, and transversely many-celled; the *Tremellineae*, in which the basidia are globose, or nearly so, and when mature divided in a cruciate manner; and the *Dacryomyceteae*, with the basidia

clavate, forked at the apex, each limb furnished with a single Under these three subfamilies the different genera spicule. are located after the following manner. (1) The Auricularieae



FIG. 60.—Auricularia mesenspores.

includes the typical genus Auricularia (Fig. 60), in which the Fungi are leathery and somewhat resemble Stereum, but with a gelatinous hymenium, which is veined in a reticulate manner. (2) Hirneola differs in the substance being more membranaceous, and often cupshaped or ear-shaped, becoming cartilaginous when dry; the gelatinous hymenium being either even or plicate. And (3) Platyglaea is wholly gelatinous, terica, with section and mostly small, erumpent or superficial, either wart-like or effused. Perhaps

the nearest relation of this small group will be found in Laschia, amongst the Polyporeae.

The most important subfamily is that of the Tremellineae, in which the basidia are subglobose. Of these, Exidia includes a variety of forms, either discoid, cup-shaped, gyrose, tubercular, or effused (Fig. 61); some of which are even, and

others papillose or spiculose. The basidia are rather ovoid, immersed in the gelatine, partite in a cruciate manner, and typically tetrasporous. Spores reniform, and for a long time continuous; at length, preparatory to germination, two or more celled, each cell producing a very short filament crowned with a narrow curved sporidiolium. In the genus Tremella the form

may be pulvinate or effused, often FIG. 61.-Exidia, with section brain-like, with sinuosities, but with-

and spores.

The basidia are globose, and divided as in out papillae. Exidia, and the spores subglobose. The promycelium resulting from germination produces globose or elliptic sporidiola. Conidia have been observed in some species, but neither spores, sporidiola, nor conidia are ever septate. In form

Ulocolla resembles Tremella, but the germinating spores are bilocular. Naematelia also resembles Tremella, but enclosing a hard central nucleus. The genus Femsjonia presents cup-shaped or pezizoid forms, with globose basidia and curved spores. In Craterocolla the form is less cup-shaped, but there are two kinds—one somewhat tremelliform, bearing basidia; the other more regular and rather truncate, bearing conidia. In Sebacinia the whole Fungus is effused like a Corticium, bearing conidia at first, and afterwards reniform spores. The genus Gyrocephalus is analogous to Guepinia; the species are erect in habit and spathulate, with basidia of the Tremella kind and pear-shaped spores. The genus Tremellodon, with the form of Hydnum but the fruit of Tremella, properly belongs here.

The subfamily Dacryomyceteae includes the lowest Tremelloid forms, in which the basidia are clavate, or nearly of the ordinary Hymenomycetal type, forked above, and each apex bearing a single spicule. The genus Dacryomycetes includes normally small pulvinate species, the spores of which are transversely or muriformly divided when mature, and the conidia (when present) growing in chains. The genera Arrhytidia and Ceracea are North American, and of minor import. Guepinia consists mostly of irregularly cup-shaped or spathulate species, with a more or less developed, and often woolly, stem. The hymenium is discoid or one-sided, and the basidia linear and bisporous. The genus Dacryomitra has the fructification of Dacryomyces, but the form and habit are those of Typhula or Mitrula, being minute and club-shaped. Collyria is a North American genus, of a single species, resembling a large Dacryomitra, with an inflated capitulum. Two or three other littleknown genera have been added provisionally to this subfamily, but their position has not yet been satisfactorily determined.

Thus closes our survey of the groups, and genera, of the *Hymenomyceteae*, in which the most distinctive features have been indicated; but there are many cross relationships and analogies which could scarcely be alluded to. It has been pertinently observed that no linear arrangement can possibly illustrate completely the relationship of the families and genera which approach each other at various points, but it is useful as a guide to the classification of corresponding forms.

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CHAPTER XIII

PUFF-BALL FUNGI-GASTROMYCETES

Every schoolboy is supposed to know what a puff-ball is, and therefore they may be accepted as a type of the peculiar order of Fungi to which this chapter is devoted. During the summer the little white puff-balls, growing in the grass of pastures and on heaths, resemble small snowballs, soft and spongy, and scarcely tinged with colour in the pulpy interior. As autumn advances the outer surface at first becomes creamy or ochraceous, covered with small warts or spines, which are readily rubbed off with the fingers. Later on the colour becomes brownish, the coating is split irregularly, or opens with a round mouth, and the interior is seen to be filled with a fine olive or purplish powder like snuff, mixed with delicate threads, called the capillitium. Such are the ordinary puff-balls which schoolboys puff in each other's faces, the distinguishing feature being that the myriads of minute spores are wholly enclosed at first within the outer case or peridium, and remain so until mature, when the coating is ruptured. The Gastromycetes, therefore, are Fungi which, as a rule, produce their spores at the apex of basidia wholly enclosed within the substance of the Fungus. They constitute a portion of the Basidiomycetes, because the spores are developed on basidia, but are specially denominated Gastromycetes, because the basidia and spores are not exposed, as in Hymenomycetes. If an ordinary Lycoperdon be cut downwards through the centre, it will be observed that the basal portion is cellular and does not contain spores; moreover, in some species this sterile portion projects upwards into the interior as a columella-which, however, is not always present. The peridium or outer coating in this instance is

double, the exterior warty, spinulose, or powdery, and the inner paper-like. In other genera, as in *Bovista*, the two coats are more distinct. In *Geaster* they are still more distinct, the outer peridium splitting in stellate rays. Thus much for the general character, but the varied modifications must be noted hereafter.

In some concise observations on this group Mr. Massee remarks that no sexual organs have been observed, but he alludes to the peculiar form of coalescence between two hyphal cells under the name of clamp-connections, which are not uncommon (Fig. 62). "A slender lateral branch," he says, " springs close to a transverse septum separating two superposed cells, and, after growing for some time, its tip comes in contact with



FIG. 62.—Clampconnections. the wall of the adjoining cell just beyond the septum, absorption of the walls takes place at the point of contact, and thus at first an open communication is established, by means of the lateral branch, between the two adjoining cells; at an early period this channel of communication is usually interrupted by the appearance of a septum at the point of origin of the lateral branch, and a second septum is in some instances formed at the point of contact with the second cell. The lateral branch is usually closely pressed to the hypha from which it

springs, but sometimes becomes arched and free from the hypha between the two points of attachment."¹

Reference is also made to the differentiation of the hyphae which are contained within the peridium. In the gleba, or hymenial pulp, of the *Lycoperdaceae* "at a very early period two sets of hyphae are present. One, thin-walled, colourless, septate, and rich in protoplasm, gives origin to the trama and elements of the hymenium, and usually disappears entirely after the formation of the spores; the second type consists of long, thick-walled, aseptate or sparsely septate, often coloured hyphae, which are persistent and form the capillitium. The latter are branches of the hyphae forming the hymenium."

There are three somewhat aberrant groups which offer

¹ Massee, Monograph of British Gastromyces, p. 4.

considerable variations in structure from the genuine puffballs. These are the *Phalloideae*, the *Nidulariaceae*, and the subterranean or *Hypogeae*. The latter come in for notice under the head of "subterranean Fungi."

The *Phalloideae*, or stink-horn Fungi, have mostly a very fetid odour, and instead of enclosing within themselves pulverulent spores mixed with threads, present externally a gelatinous mass of agglutinated spores, which is collected upon some superior and exposed surface. The whole number of described species in this family is about eighty, and they are most common in warm climates. Some are stipitate and others clathrate or latticed, but all are at first enclosed in a general volva of an egg-shape, with a gelatinous inner stratum. The entire plant is of a soft, watery texture, quick in growth, and rapid in decay. As the gelatinous darkcoloured mass of the hymenium is greedily devoured by insects, it is reasonably assumed that it is by this agency that the spores are dispersed.

Mr. T. Wemyss Fulton devoted some attention to this subject,¹ and the following is a digest of his observations, entirely confined to the common stink-horn, Ithyphallus impudicus, which grows freely in woods and gardens :--- "The hymenophore or reproductive portion consists, in its earliest stages, of minute swellings, which arise on the underground mycelium. These at first are homogeneous, but gradual differentiation goes on, so that towards maturity the following parts may be (1) An enclosing cortical portion, the volva or recognised. peridium, composed of three layers-an outer firm skin, an inner thin membrane, and an intermediate gelatinous layer. At the base there is a cup-shaped portion, which supports the stem, and is continuous by its margin with the peridial layers, and below with the mycelium. (2) A central medullary portion, composed of two very different structures, the gleba or spore-bearing part, which forms a hollow conical cap, lying within the inner peridium, and surrounding the upper portion of the stem, to the apex of which it is attached. Its outer surface bears the hymenium, and is honeycombed by a number

¹ "Dispersion of Spores of Fungi by Agency of Insects, with special reference to the Phalloidei," by T. Wemyss Fulton, in *Annals of Botany*, vol. iii., 1889.

of irregular depressions, in which the mass of spores is lodged. The stem, consisting of a cylinder whose walls at this stage look firm and solid, is composed of a multitude of small compressed cells filled with jelly.

"The volva is at first concealed beneath the surface of the soil, but towards maturity it breaks through the ground, and the exposed part gradually becomes conical, and finally ruptures, the stem rapidly lengthening and elevating the gleba in the air. The gelatinous contents of the flattened cavities disappear, and they become dilated, the previously compact stem increasing threefold or fourfold in magnitude, and becoming open and spongy, the cavities being distended with air. The elevation of the gleba takes place with great rapidity, and may be completed in half an hour or from two to three hours, attaining a height of from six to ten inches. The utility of this sudden elevation by a mechanical process, instead of the slower process of simple growth, will hereafter be evident (Fig. 63).

"At the time of emergence, and for a brief interval after,



FIG.63.—Ithyphallus impudicus.

the hymenial surface is firm and solid, greenish gray in colour, and emits a faint, mawkish, but sweetish and honey-like odour, which is attractive to house-flies. Very soon, and before the elongation of the stem is completed, it begins to darken, the odour becomes fetid, and the consistency changes so that it gets rather sticky and tenacious. A little later it is dark green, almost black, the odour is strong and repulsively fetid, and in consistence slimy or almost fluid. These changes begin at the apex and proceed downwards; they seem to depend largely upon the influence of light, for if one side be protected from its action the change in consistency and colour is retarded on that side. When examined microscopically the fetid fluid is seen to contain myriads of spores

(each 3 μ . long). These changes occur during the hot months of the year, from the early part of July till the end of September, at a time when insect life abounds.

"As soon as the strong, dung-like odour is developed, the

PUFF-BALL FUNGI-GASTROMYCETES

liquefying hymenium is visited by large numbers of flies, which sometimes almost cover it, and suck up the fluid mass with great avidity during hot sunny days; but when the weather is cloudy or cold, fewer flies are to be seen."

Examinations were made of flies taken from the deliquescing gleba, and thousands of spores were found adhering to the feet and proboscis. The flies placed in confinement showed that their excrements were almost exclusively composed of spores. To determine if the excrementary spores retained their vitality they were placed in tubes on sterilised earth. The tubes were then closed with cotton-wool and buried with the contained spores, and different substances with them. In about two months the spores had germinated, and in some produced a plentiful mycelium. Hence it is clear that the spores after passing through the stomachs of insects do not lose their power of germination.

This family is remarkable for the prevalence of a bright red colour near the hymenium, and also for the peculiarity of many of the forms. In *Dictyophora*, *Ithyphallus*, and *Mutinus* the form is columnar and phalloid; in *Clathrus* and *Colus* it is clathrate. In *Calathiscus* and *Aseröe* the disc is stellate, and in *Kalchbrennera* it is coralloid. The spores in all the species are very profuse and minute, generally involved in mucus.

In the family of *Nidulariaceae* we meet with other peculiarities, and of these the common species of Cyathus or Crucibulum, called the "bird's-nest Fungus," may be taken as the type (Fig. 64). There are altogether only about sixty described species, and the family, under some of its forms, is pretty widely distributed. When mature the Fungus is not more than from one to two centimetres high, and resembles in form little inverted bells, at first covered across the mouth with a white membrane or operculum, which when ruptured exposes a number of lentil-shaped bodies, packed like eggs in a little bird's-nest. These are the peridioles, each of which is attached to the inner surface of the cup by a long elastic cord, proceeding from the under face of the sporangiole. Each of these sporangioles, when cut in section, reveals a central cavity, into which the basidia project, with their

attached spores. These lentil-shaped bodies are analogous to the peridiola in such genera as *Polysaccum* and *Arachnion*,



FIG. 64.—Crucibulum vulgare. After Greville.

but all the intervening plasma has been dissolved away, so that they remain free within the peridium. In all the species the sporangioles are very hard and firm when mature, and the contents are never powdery. In some species the external peridium has a squamose or hairy surface but in a few species it is nearly smooth. Sometimes the upper third of its length is marked with conspicuous parallel channels or striae. In Cyathus the peri-

dium is composed of three superimposed layers, and in *Crucibulum* of two.

Having disposed, in a summary manner, of these two families, we return to the Trichogasters which form the bulk of the order, and especially the *Lycoperdaceae*. Probably the genera which contain the largest number of known species are *Lycoperdon*, *Geaster*, and *Bovista*. In these the peridium is more or less distinctly double, but there are allied genera in which the peridium is simple. The delicate threads, found mixed with the spores when mature, forming the capillitium, are an important element in classification. In the mature gleba they seem to be entangled, and indefinite as to their origin in *Lycoperdon* and *Bovista*, but in other genera they distinctly radiate from the columella to the inner wall of the

PUFF-BALL FUNGI-GASTROMYCETES

peridium (Fig. 65). This columella is only a continuation of the spongy base in Lycoperdon, but in Diploderma it is hard and

woody. In some species of *Geaster* the columella is distinct and clubshaped, extending half-way up, with the threads of the capillitium radiating towards the periphery. De Bary has described the complex peridium of *Geaster* in the following terms :— "*Geaster hygrometricus* is up to the period of perfect maturity a roundish body, which may be of the size of a



FIG. 65.—*Lycoperdon*, with sterile base and columella.

hazel-nut, and remains beneath the surface of the ground. Six layers may be distinguished in the peridium in a vertical longitudinal section a short time before the compound sporophore is mature (Fig. 66). The outermost layer is of a brownish colour, flaky and fibrous, and is continued on one side into the mycelial strands which spread through the soil, and on the other passes into the second layer; a thick, stout, brown membrane entirely covering the compound sporophore. This is followed towards the inside by a white layer, which is more largely developed at the base of the compound sporophore than elsewhere, and is immediately continuous at that



FIG. 66.-Geaster.

spot with the inner peridium and the gleba. Both of these last-mentioned layers are formed of stout, closely-woven hyphae running in the direction of the surface, and may be combined under the name of the fibrillose layer. The inner of the two is lined on the inside by the collenchyma layer, ex-

cept where its basal portion passes into the gleba. This layer is cartilaginously gelatinous, and consists of hyphal branches of uniform height, connected together, without interstices, which are placed palisade-like vertically to the surface, and are bent as they spring from the hyphae of the fibrillose layer. The strongly-thickened stratified walls of the

155

cells of this layer have great capacity for swelling. Inwards from the collenchyma is a white layer, the innermost region of which is the inner peridium, while the outer, which may be called the split layer, consists of soft, loosely-woven hyphae. which pass at many points into the inner peridium. When the fungus is quite matured, the outer peridium, through the influence of moisture and the swelling of the collenchyma layer, bursts outwards from the apex in a stellate manner, forming several lobes, which turn back, so that the upper surface, which is covered by the collenchyma, becomes convex. The split layer is by this means so torn to pieces that its constituent parts remain hanging as perishable flakes, some to the collenchyma, some to the inner peridium. It is known that the collenchyma layer retains its hygroscopic qualities a long time, and the outer peridium remains a long time lying on the soil, stellate in shape, spreading out its rays in moist weather, and bending them inwards when dry. The flaky investment of the outer peridium is often more strongly developed in G. fimbriatus and G. fornicatus, and in the latter it is composed of the finest of hyphae; it tears away from the fibrillose layer when the peridium is ruptured, and lies on the ground, beneath the peridium, as an open empty sac. The extremities of the lobes remain for the time firmly united to the margin of this sac, and as the collenchyma layer expands greatly, the star formed by it and the fibrillose layer, especially in G. fornicatus, becomes convex upwards, and carries the inner peridium on the apex of the convexity."¹

The genus *Calostoma*, when carefully examined, shows many points of affinity with *Geaster*. Massee has given full details of its morphology,² which should be perused *in extenso*, but the following is a summary. On the authority of Hitchcock it is stated that in *Calostoma cinnabarinum* the Fungus on bursting from the soil is enclosed in a gelatinous envelope, like *Ithyphallus impudicus*, nearly a quarter of an inch in thickness. This immediately bursts, even before the whole body of the Fungus has risen above the ground, and the exterior part of it

² Massee, "Monograph of the Genus Calostoma," in Annals of Botany, vol. ii. p. 25, 1888.

¹ De Bary, Fungi, etc., English edition, p. 316.

PUFF-BALL FUNGI-GASTROMYCETES

falls upon the soil around the Fungus in the form of a viscid jelly, and is ere long absorbed in the earth. The short stemlike base arises from a few firm white mycelium strands, composed of thin-walled, sparsely septate, branched threads. After removal of the external gelatinous volva a vertical section shows an external colourless zone, separated from the inner portion, except at the base, by a thin red line. The outermost zone is composed of thick-walled, mostly aseptate, densely interwoven hyphae, passing through the red zone into the central less compact portion, where they are mixed with thin-walled, septate, branched hyphae having numerous slightly thickened free tips.

When dry the plant is rigid and cuts like horn; a median vertical section in this condition shows the external wall to consist of three distinct layers-the two outermost confluent at the base, the innermost free below, but in contact with the middle layer at the umbonate apex. The external layer or exoperidium is at first continuous over every part of the plant, and thinnest at the apex. The red streak is now seen to form the innermost portion of the exoperidium, and at the present stage of development exists in the form of red powder. In the earlier condition the cells forming the red zone are thickwalled, the substance of the walls being studded with numerous small red granules. Eventually the walls of the cells constituting this zone become mucilaginous and disappear, leaving the red granules in the form of a fine powder, thus effecting the separation of the exoperidium from the originally homogeneous spherical weft of hyphae. The innermost portion of the exoperidium consists of compactly interwoven, thickwalled hyphae, not at all mucilaginous, and furnished with a few red granules, which become rarer towards the outside, and eventually disappear; the hyphae at the same time becoming thinner and thinner, owing to the diffluent walls, and at the outside entirely converted into mucilaginous jelly.

Owing to a slight increase in length of the basal portion, between the exoperidium and endoperidium, and continued increase in the size of the latter, the exoperidium is ruptured at the apex in an irregularly stellate manner, the lobes when moistened curling inwards, and soon breaking away at the

base. In most species the exoperidium becomes completely disorganised, often remaining in the form of warts on the endoperidium. When dry the endoperidium is cartilaginous and brittle, of a dirty ochraceous colour, becoming much swollen when moistened. It consists, when young, of thickwalled, more or less gelatinous hyphae; later on the thick walls become disorganised, and present the appearance of a loose weft of hyphae imbedded in mucilage, but in reality the apparent hyphae are the lumina of the original thick-walled cells.

When young the wall of the endoperidium is of equal thickness, but during spore-formation local growth takes place at the apex, forming a cylindrical umbo, the circumference of which is furnished with several deep vertical furrows. At this stage a red streak appears in the median line of each vertical ridge dividing the furrows, these streaks being continued along the apical portion of the ridge and meeting in the centre. These streaks extend through the entire thickness of the wall, and form a central core down the umbo, the hyphae becoming disintegrated as in the red zone. Resulting from this process is the formation of a mouth, the surrounding teeth remaining closed until the period of dehiscence, when the separation of the teeth takes place, the margins and inner surface being covered with red powder. The endoperidium is not differentiated from the exoperidium at the base. There is no trace of a columella. The innermost layer, or spore-sac, is yellowish white and flexible, perfectly free from the endoperidium, except at the apex, where it remains attached to the inner surface of the teeth. During spore-formation the central mass, or gleba, is continuous with the inner wall of the spore-sac. There are irregular cavities, and the basidia produce five or six spores on wart-like projections at the apex. The spores are globose at first, and colourless, then elliptical, pale, ochraceous, and minutely warted.

When the spores are ripe the basidia and the trama dissolve into mucilage; the gleba contracts, but still remains attached to the apex of the peridium; ultimately the mucilage contracts and dries into irregular masses, leaving the spores quite free. In the normal mode of dehiscence the spore-sac and its contents appear to pass out at the mouth and remain attached to the teeth of the endoperidium; but sometimes the spores are expelled without extrusion of the spore-sac. In all species every part of the plant, with the exception of the spore-sac, is perfectly rigid and cartilaginous when dry, every part except the inner surface of the endoperidium becoming swollen and more or less mucilaginous when moistened. The stem-like base increases in growth when the spores are mature.

In *Battarrea* De Bary has shown that the whole development, up to the maturing of the spores, is passed while still enclosed in the volva; and when this is ruptured by elongation of the stem, a portion of the volva is usually carried up on the surface of the circular peridium, which is more or less erescent-shaped in section (Fig. 67). Finally the peridium splits along the margin, the upper portion falling away, and leaving the spores exposed on the lower persistent part, from which they are soon blown away.

In *Tylostoma* also the differentiation of the gleba takes place underground. When the spores are mature the stem

elongates. This elongation is due to increase in length of the central portion, the outer or sheathing portion being cracked transversely, one portion remaining below and sheathing the base, the other forming an abrupt termination of the base of the peridium like a collar at the apex of the stem.

One of the most interesting genera of the stipitate forms is *Podaxis*, which is a native of warm climates, being particularly associated with the nests of Termites. In this genus Mr. Massee contends that the spores are produced in sacs or asci, and infers that therefore they belong systematically to the *Ascomycetes*; but with this inference we do not agree. Although the spores are at first enveloped in cysts, it by no means follows that this establishes an affinity with *Ascomycetes*, but only an analogy.



FIG. 67.— Battarrea.

The species of *Podaxis* bear an external and superficial resemblance, in size and form, to unexpanded specimens of *Coprinus comatus*: the upper elliptical, spore-bearing capitulum

159

being borne upon a long cylindrical stem, gradually attenuated upwards, into and up to the apex of the capitulum, like a columella; the differentiation of the gleba, until the maturity of the spores, taking place while the Fungus remains under ground. There is an absence of the sinuous cavities, bounded by well-defined tramal plates, so characteristic of Gastromycetes, but from the earliest condition, according to Mr. Massee, "the gleba presents a sponge-like structure, its very irregular walls consisting of thin-walled, sparsely-septate hyphae, originating as lateral branches from the hyphae forming the central axis or the inner portion of the outer protective wall. Mixed with the colourless, thin-walled hyphae are others which originate from the hyphae of the axis; these eventually become coloured, and form the capillitium; the thin-walled, colourless hyphae forming the irregular walls of the gleba send into the interstices numerous long, lateral branches; these branches-the ascogenous hyphae-are aseptate, have very thin colourless walls, are richly supplied with granular vacuolated protoplasm, and at the tips produce two or more short branches, which in turn emit short secondary branches, the whole forming a compact tuft; these terminal branches differ from the parent hyphae in being broken up into numerous short cells by transverse septa; each component cell produces a lateral outgrowth, at first papillaeform, then cylindrical, and eventually broadly obovate, and attached to the parent cell by a narrow neck; these terminal cells-the asci-after receiving all the protoplasm from the parent cell, are cut off from the latter by the formation of a septum across the narrow basal portion. Owing to the fasciculate arrangement of the terminal branches the asci are densely crowded, varying in number from ten to fifty, or even seventy on specially vigorous heads. The asci are developed in succession, and it is not unusual to meet with empty shrivelled asci, others with the spores not yet differentiated, and others quite young, in the same cluster. I am inclined to believe that the short ascigerous branches are also produced laterally on the aseptate hyphae, but am not certain on this point. The asci are usually constant in form and size, but now and again an exceptionally large one may be seen, and sometimes one or more lateral prominences disturb the

PUFF-BALL FUNGI-GASTROMYCETES

usual symmetry of outline. The asci are normally monosporous, but occasionally two spores are produced, especially in the extra large or deformed examples, when the spores are differentiated; but before attaining their full size, and while yet quite colourless, they escape from the asci through an irregular slit, the latter persisting in the shrivelled form seen on examining the hymenium of mature specimens. The spores, when mature, are broadly elliptical, or sometimes subglobose (averaging $10 - 12 \times 9 \mu$), perfectly smooth, and of a deep translucent brown by transmitted light, and furnished with a single welldefined germ-pore. When the spores are first liberated the colour of the gleba is very pale yellow; from this condition the coloration passes through primrose yellow to clear brown, and eventually dark brown, as seen in the mass. When young the hyphae of the capillitium are colourless, straight, rarely branched, and in this condition there is little or no indication of the spiral marking so conspicuous at maturity; during the development of the gleba the capillitium threads pass through the same sequence of coloration as already described for the spores, commencing with pale yellow and ending with bright After the formation of the spores, the compact basal brown. portion, below the point of attachment of the lower margin of the peridium to the central axis, elongates into a hollow stem, eight to ten inches high, elevating the yet closed peridium far above ground. The ripening of the gleba, as shown by the progressive coloration of the spores, commences at the base, and nearest the axis, and progresses towards the apex. When the spores are mature, and the capillitium fully developed, the ascogenous hyphae, with the clusters of shrivelled asci, can still be seen, and although usually colourless, are in some instances more or less tinged with brown. In the clusters of split shrivelled asci are others that present no split or fracture in the wall; these are homologous with the so-called sterile basidia or paraphyses. At this stage the peridium breaks away from the stem at its lower point of attachment, the margin being irregularly torn, when it resembles a halfexpanded Agaric; eventually the whole of the dry and brittle peridium breaks away, and the stem remains with its blackishbrown mass of spores and capillitium, resembling a bulrush, the

11

final dispersion of the spores being effected by the wind and rain." 1

In seeking for the affinities or analogues of the species of *Podaxis*, Mr. Massee thinks that these should be traced through the subterranean *Gastromycetes* to the ascigerous *Elaphomyceteae*. "I have shown," he writes, "the gradual conversion of the ascigerous *Tuberaceae* into the basidiosporous *Hymenogastreae*, due to the changes of asci into basidia, and the subsequent evolution of the whole of the above-ground *Gastromycetes* from the subterranean ascigerous *Tuberaceae* through the *Hymenogastreae*; and now we find a second attempt on the part of the *Tuberaceae* to evolve an above-ground branch through the *Elaphomyceteae*, and continued by the genera *Podaxis*, *Tylostoma*, and possibly *Battarrea* and *Queletia*.

He might further have indicated that in another direction, through Secotium, Polyplocium, and Montagnites, the Gastromycetes are linked to Coprinus, and, through that genus, with the Agaricini. Montagnites, or as sometimes called Gyrophragmium, has in some systems been included with Hymenomycetes in a position next to Coprinus, to which it bears some resemblance.

The Sclerodermeae are a group which seem to fall into an intermediate position between the Lycoperdaceae and the subterranean Gastromycetes-a fact which was recognised by Mr. Massee when he indicated that they differed from the former in the absence of a capillitium and in the indehiscent peridium; and from the latter in not being subterranean, although there are one or two species in which subterranean individuals are sometimes to be met with. "As in the Hymenogastreae, the peridium is thick, usually warted or rugulose externally, and but little differentiated, the trama springing from every part of In Polysaccum the cavities of the gleba are its inner surface. comparatively large and uniform in shape, being more or less polygonal in section. The walls of the trama are bright yellow In this genus the peridium appears to be in most species. completely formed at a considerable distance underground, as some species have a stout stem-like base, from eight to ten inches long and completely buried in the ground, the peridium alone appearing at the surface. From what is known in other

¹ Massee, "Monograph of the Genus Podaxis," in Jour. of Botany, March 1890.

PUFF-BALL FUNGI-GASTROMYCETES

instances, the stem probably remains rudimentary until the spores are matured, when it elongates for the purpose of raising the peridium to the surface, thereby facilitating the dispersion of the spores."¹

The subterranean Gastromycetes, which technically belong here, are treated in the chapter on subterranean Fungi, because of their similarity in habit and appearance; but for all this they must not be confounded, and cannot be if the fructification is properly remembered.

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¹ Massee, "Monograph of British Gastromycetes," in Annals of Botany, vol. iv. (1889), p. 11.
CHAPTER XIV

ASCIGEROUS FUNGI-ASCOMYCETES

WHATEVER the form which the receptacle may assume, the Ascomycetes have always this one feature in common-that the spores are not naked or exposed, but are always enclosed within a delicate external membrane or spore-sac, and these latter are imbedded in the modified hymenium. It is quite true that the hymenium itself may be exposed, but the spore-sacs, or asci, are imbedded, and the spores are not visible externally until they are mature and discharged. It was proposed some years since that the term spore should be applied only to such reproductive bodies as were produced naked, or not enclosed in an investing membrane, whereas all such reproductive bodies as were developed within an ascus, or investing sac, should be termed sporidia. It will be obvious to all who consult the most recent works, that this distinction has not been maintained, at least with the old limitation; so that conidia, spore, and sporidium are employed without recognised definition, almost, if not entirely, as if they were synonymous. We still hold that the spore which is produced naked, whether as a basidiospore or stylospore, should possess a name by which it may at once be distinguished from such as are developed within an ascus, whether it be ascospore, sporidium, or some equivalent. When Saccardo elaborated his extensive work Sylloge Fungorum he recognised this difficulty, and at the commencement of the third volume defined the terms which he should employ, and accepted sporidia as exclusively applicable to Spore, simply and without prefix, was practically ascospores. the same as basidiospore, for he applied it to all the Hymeno-These were the two distinctive terms for the primary mycetes.

ASCIGEROUS FUNGI-ASCOMYCETES

groups of complete Fungi to recognise the spores. The Uredinei had special terms for the different stages of the cycle, as commonly in use. The imperfect Fungi with naked exposed fructification, as Hyphomycetes, appropriated the term *conidia*. The other imperfect Fungi, in which the fructification was more or less enclosed in a perithecium, cup, or cell, such as the Sphaeropsideae, have spore-bodies with the name of *sporules*. By adhering to these terms much trouble and confusion will be spared to the student when he comes to consult systematic works for himself.

The lowest and simplest form of Ascomycetes is to be found in the genus Ascomyces or Exoascus, in which the asci are not compacted into a hymenium, but are loosely arranged upon a delicate mycelium, without any definite receptacle or excipulum being present. In the more typical forms the mycelium gives rise to a receptacle of some kind, either closed or open, in which a compact hymenium is developed, and the whole Fungus assumes a definite and determinate form. From certain features in this receptacle the entire Ascomycetes may be classed in three or four distinct groups, and are thus characterised :- Pyrenomyceteae, with a distinct perithecium, which is at first closed, but at length opening by a pore at the apex, or dehiscing by fracture, so as to allow the mature sporidia to Discomyceteae, often fleshy or waxy, with a discoid or escape. cup-shaped excipulum, soon expanded, and exposing a plane or concave hymenium, from which the sporidia are ejected when Hysteriaceae, intermediate between Pyrenomyceteae mature. and Discomyceteae, substance more or less coriaceous, at first closed, afterwards dehiscing by an elongated mouth, gaping when moist, and then exhibiting a compact hymenium. Allied to Pyrenomyceteae by the coriaceous excipulum and the connivent lips of the orifice, through such a family as Lophiostomaceae; but with a tendency towards Discomyceteae in the compact. hymenium, which becomes exposed when moist, and is thus suggestive of Phacidiaceae. Finally, Tuberaceae, in which the Fungus is normally subterranean and fleshy, the internal substance containing irregular cavities or cells, the walls of which are lined by the hymenium; never dehiscent, so that the sporidia are only liberated by the decay of the entire Fungus.

This group is allied to the *Discomyceteae* by such genera as *Sphaerosoma* and *Bergrennia*, and analogous to the *Gastromycetes*, especially *Scleroderma*, through the family of the *Hypogeae*.

The hymenium consists usually of two kinds of organs, which stand side by side, closely packed together; these are



FIG. 68.—Asci and paraphyses.

the asci and the paraphyses, but the latter are sometimes, although rarely, suppressed. The asci are essentially membranaceous, delicate, colourless sacs, mostly closed, but occasionally dehiscing at the apex by an operculum or lid, more commonly irregularly ruptured, to permit of the escape of the sporidia. These asci have either a clavate form, with a more or less elongated base, or they are cylindrical, of nearly equal breadth throughout, except at the base, where they are narrowed downwards to the dimensions of the supporting hypha. In some families, such as the Perisporiaceae, as well as in the Tuberaceae, a form of ascus prevails which approaches to globose or pear-shaped. All forms of asci are usually very numerous in each hymenium, but the globose are less so than the clavate or cylindrical. The form that is peculiar to any species is persistent in that species, so that the form and approximate size are relied upon as having value in the Whatever the form determination of species. each ascus assumes, it normally encloses eight sporidia, or some multiple of eight-as sixteen,

thirty-two, etc.—occasionally only four, more rarely only two, and very rarely indeed only one. In cylindrical asci the sporidia may be expected to range themselves in a single row, but in clavate asci they are either biseriate or irregularly grouped towards the upper portion of the ascus. By far the larger number of sporidia are continuous, consisting of a single cell, and range from a globose to an elliptical form, especially in the *Discomyceteae*, whilst in the *Pyrenomyceteae* greater variation prevails. Doubtless all the forms of sporidia are at first continuous, and acquire septa as they approach

ASCIGEROUS FUNGI-ASCOMYCETES

maturity. Thus a sporidium may at first be one-celled, then it acquires a central septum and is two-celled; each of these cells may be again divided, so that the sporidium becomes triseptate, and by a further process of subdivision the triseptate sporidium may ultimately become seven-septate. By means of a less symmetrical subdivision we have also biseptate, four or five septate, and even muriform sporidia, with the cells divided in both directions. Whatever the number of cells into which a sporidium may be divided, each cell appears to be a reproductive unit, capable of germination and producing its kind; so that each septate sporidium is in itself compound-that is to say, each of its component cells acts in the same manner as a simple, undivided sporidium would act. The forms of sporidia are so numerous that it would be tedious to enumerate them here. Some of these are externally rough, but the majority are smooth, and they may be hyaline or coloured. In the Discomyceteae coloured sporidia are comparatively rare; the coloration is confined to the epispore in all cases, and the contents remain colourless.

Paraphyses are more slender than asci, with which they are associated, being placed side by side with them in the hymenium, and, when present, are more numerous than the asci, and usually a little longer, but filiform or thread-like. There has from time to time been much speculation as to their functions and relationship. Some have regarded them as abortive asci, amongst whom was the late Rev. M. J. Berkeley, who wrote : "The essential character of this important division consists in the development of definite or indefinite sporidia within certain of the external cells of the hymenium, called asci, which are frequently accompanied by inarticulate or septate, simple or branched threads, which are abortive asci, known under the name of paraphyses." This opinion seems to have been based chiefly upon the occurrence of organs, apparently paraphyses, mixed with normal paraphyses and asci in the hymenium of certain Discomycetes. These bodies presented inflations at the apex or below it, such inflations enclosing a sporidium resembling the genuine sporidia in neighbouring asci; and hence it was concluded that these abnormal bodies were degraded asci, not yet fully degraded into paraphyses.

It must be borne in mind that paraphyses are developed first, and afterwards the asci; that the paraphyses are often septate, whilst asei are not; and that they seem to possess functions of their own. Another theory is that the paraphyses are sometimes, if not always, styles or peduncles surmounted by conidia—that is to say, that they are conidiophores. The hymenium of *Tympanis ligustri* has been seen bearing normal asei and paraphyses, but amongst the paraphyses other and shorter ones, surmounted by brown uniseptate conidia, one to each filament. The inference that therefore paraphyses are conidiophores cannot be maintained on such a basis without stronger corroborative evidence.

Paraphyses are more highly developed in the Discomyceteae than in any other of the Ascomyceteae, and the following forms have been indicated—*i.e. Linear paraphyses*, which are the simplest form. They consist of a slender cylindrical cell of equal thickness throughout. Sometimes they but little exceed the asci in length, and then remain perfectly straight, but when considerably exceeding the asci the tips are often more or less curved as soon as they are set free, so that the retractile tendency can exhibit itself. Such paraphyses are usually colourless and without evident contents, but at times a row of nuclei exhibit themselves, or the threads become septate. These may be free of each other, or they may be agglutinated together by hymenial gelatine.

Clavate paraphyses are those which expand in their upper portion into a more or less club-shape. Sometimes the expansion is very gradual, occupying the upper half of the paraphyses; at others it is more abrupt, and at least three-fourths of the paraphysis remains linear. Gradually this form merges into the capitate form, and usually the thickened apex is filled with a granular plasma.

Capitate paraphyses are those in which the apex is suddenly expanded into a pyriform, obovate, or subglobose head. This knob contains at times a single large globose guttule, perhaps an oil-drop; at others it contains a granular protoplasm. The colouring of the upper portion of the paraphyses may be due to the coloured contents, but in some instances it is caused by the coloured investing gelatine.

ASCIGEROUS FUNGI-ASCOMYCETES

Acuminate paraphyses are confined to such minute hairy Pezizae as formed a portion of the old series Dasyscypha before the large genus Peziza was broken up into small genera. They are slender, thickest in the middle, and diminished towards either extremity, so as to be narrowly fusiform, with the apex acutely pointed. As they are considerably longer than the asci, they project on the hymenium and impart to it a velvety appearance.

Branched paraphyses may be met with amongst linear, clavate, and capitate paraphyses, but not the acuminate, which last are always simple. Usually the branching is a simple furcation, with the branch reaching to the same height as the main stem. Nodulose or inflated paraphyses are rare, such as are found in *Peziza sterigmatizans* and *Otidea apophysata*; but in these cases they do not seem to be accidental, but normal, and therefore incidentally valuable in the determination of species. In other species abnormal developments of paraphyses have been seen and figured, but they are not permanent to the species, and seldom to be met with, so that they cannot be considered as other than abnormal developments.

Dissilient paraphyses are those in which the upper joint or joints when mature break off, and give a pulverulent appearance to the disc. They are not uncommon amongst the *Patellariaceae*. There seems to be no valid evidence that the cast-off cells partake at all of the character of gonidia, or are capable of germination.

The functions of paraphyses appear to be mainly the protection of the fructiferous organs. Surrounding the asci, they seem to stand in a similar relationship to them as in flowering plants the corolla bears to the essential organs. They constitute in the earlier stage of growth the entire hymenium, and in this stage form a disc with their upper extremities, as witnessed in the Discomycetes; whilst their parallel sides, immersed in a gelatinous fluid, afford ready channels for the growth and development upwards of the sporidiiferous asci. It can readily be imagined that such a structure affords very great protection for the asci during growth. It can hardly be supposed that delicate asci could successively be produced on

an entirely exposed surface without great risk of destruction; but by means of this arrangement they thrust themselves upwards through protecting channels, lined everywhere with a lubricative fluid, so that their movements are facilitated as well as protected. It is an undoubted fact that all the asci of an hymenium are not developed at once, but proceed for some time in a regular succession from the subhymenial tissue. At first the asci are slender, gradually increasing in volume as they rise, but until they have attained their full height their contents are plastic and granular. Having approached their adult stature, the differentiation of the protoplasm takes place; gradually the outline of the sporidia is indicated, commencing at the summit of the ascus and progressing downwards; and finally the sporidia are formed. It is well to bear in mind that the terminal sporidia are the first to be matured, and this is conspicuously evident when the sporidia are ultimately coloured; under favourable circumstances a delicate gradation of colour will be observable downwards through the whole series. It has already been remarked that it is of rare occurrence that the asci should reach by their apices the surface of the disc. As a rule the paraphyses, being the longest, extend above, and still protect the asci. The swollen or clavate tips compensate to some extent for the space occupied below by the asci, and the surface is still maintained imper-In cases where the tips of the paraphyses are not vious. clavate but filiform, they are not unusually branched in their upper portion, which only adds to their volume; and in some cases the extremities are bent, curved, circinate, or interwoven, so that still the whole disc is covered, and no openings left above the apices of the rising asci. Undoubtedly the apices of the asci are always most free from pressure or restraint, which is essential to the free discharge of the mature sporidia. It may sometimes be seen on the field of the microscope that, as a mature sporidium is expelled from the apex of its ascus, the clavate paraphyses which surround it are parted by the force of the eviction, but immediately resume their old position again with a jerk, as if impelled by their own elasticity. These observations have been made, of course, on such Ascomyceteae as have the disc exposed, but by analogy we may infer that the process is similar, if slightly modified, in all.

It has already been intimated that the highest development of paraphyses is found in *Discomyceteae*, or such of the *Ascomyceteae* as have the disc exposed, and we would suggest that their function in such cases, in part at least, seems to be the protection of the disc, or rather the apices of the asci, and to prevent too great evaporation consequent upon the exposure of the hymenium. In closed perithecia, such as are found in *Pyrenomycetes*, the paraphyses are often insignificant; and in the *Tuberaceae*, which are wholly immersed and preserved from the light, paraphyses are as nearly as possible obsolete. All which tends to support the theory of the functions of paraphyses above suggested.

The relationship of the Ascomyceteae with the other orders of Fungi has been the subject of some speculation, and has originated more than one theory, which we need not stay to discuss. The Ascomyceteae and the Basidiomyceteae may be two parallel groups, and we will leave them at that, but the Ascomyceteae have in some of their species been shown to be associated with such imperfect Fungi as the Hyphomyceteae, the Sphaeropsideae, and the Melanconieae; but because some of the species are known to be so related, it is taking too hazardous a leap to affirm that all the latter are merely transitional forms of the former, and should not be regarded as autonomous. Massee has truly said, in reference to this subject :--- "The divisions called Melanconieae, Sphaeropsideae, and Hyphomyceteae include over eight thousand species from all parts of the world. Out of this number less than one hundred have been clearly proved by cultures to be forms of species belonging mostly to the Ascomyceteae; yet on the strength of this small percentage of proved cases, the three groups are entirely omitted in the schemes of classification given by De Bary and Brefeld, implying that all are considered merely as form-species-a supposition which may be quite correct, but is far from being proved, and not altogether countenanced by the investigations of these same authors, who claim to have shown that in some of the Ascomyceteae the gonidial stage is completely lost. De Bary and his followers do not, as a rule, accept the 'special creation'

theory, but, judging from their writings, consider that species are evolved by certain processes of differentiation from previously existing species. If so, assuming that the gonidial stage of an originally pleomorphic Fungus alone remains, the ascigerous condition having been entirely arrested, should the gonidial form still be considered a phase of a higher form that has no existence, or, being capable of carrying on an entirely independent existence, will it ever be entitled to rank as a species ? If not, then, from the evolution standpoint, all living organisms, from analogy, are merely forms of a primitive progenitor. From the above it will be seen that in a systematic work the *Sphaeropsideae*, *Melanconieae*, and *Hyphomyceteae* must be admitted; and until their affinities are demonstrated by direct experiment, not analogy, it will be well to use the terms genera and species in the ordinary sense."¹

¹ British Fungi-Phycomycetes, etc., by G. Massee, p. 65. London, 1891.

CHAPTER XV

DISCOID FUNGI-DISCOMYCETES

This is one of the most interesting groups of the Ascomycetous Fungi, in which the sporidia are contained in membranaceous sacs, or asci, and when mature expelled from the apex, often in a little smoky cloud, under the influence of sunlight. The normal appearance is that of a cup or saucer, at first deeply concave, but at length more or less expanded and flattened, ranging in size from that of a pin's head to several inches. The hymenium, or spore-bearing surface, is uppermost and soon exposed, very often of a bright and attractive colour. We may assume that this bright coloration is of some service to the plant, but at present that use has not been determined. One important feature, in which the majority of the discoid Fungi differ from the majority of the Pyrenomycetal Fungi, is in their fleshy or waxy substance, which is modified in one direction until it becomes soft and tremelloid, and in the other direction it is rather tough and leathery, but never really brittle and carbonaceous.

It will be better, in the first instance, to attempt a description of a typical discoid Fungus such as was formerly known by the name of *Peziza*, although the old genus *Peziza* is now broken up into a number of smaller genera. The general form, when young, is either globose, or when possessed of a stem, clavate, or club-shaped, pierced with a pore at the apex. As growth proceeds, the pore enlarges and the head gradually becomes cup-shaped, so that the Fungus resembles a wine-glass; the disc or lining of the cup flattening with age until it is almost a plane surface. The outer surface, or *excipulum*, as

sometimes called, may be hairy, woolly, granular, or quite smooth (Fig. 69).

The inner stratum, or disc, has quite a different structure from the outer stratum, or excipulum, being composed of a



section and ascus.

series of elongated, delicate cells like cylinders, closely packed side by side, their apices terminating in the disc, and their bases being seated upon the inner surface of the excipulum (Fig. 70). In due time these cylindrical sacs, or asci, contain four or eight, or some multiple of that number, of smaller bodies, which are the spores or sporidia-the reproductive corpuscles of the Fungus. In some cases the apex of the ascus opens FIG. 69.-Cup of Peziza, with by means of an operculum, or small

lid, but at others by an irregular rupture, to permit of the escape of the spores. Mixed with these spore-bearing sacs will be found a number of long thread-like bodies of equal length, or longer than the asci, and these are termed paraphyses. Some mycologists believe them

to represent abortive asci, and this is supported by the fact that now and then a paraphyse is observed which encloses one or two spores, like the normal spores of the Fungus. When the Peziza is young, and the cup is closed, all the cylindri-



FIG. 70 .- Section of cup of Ascobolus.

cal cells are narrow, thread-like, and empty ; but as growth proceeds and sporidia begin to form, the diameter of the cells increases, and, as a consequence, the disc enlarges and expands with the lateral pressure so as to occasion the flattening out of the cup. When there is a great expansion the edges of the cup are either split or bent back, so that the disc becomes convex, all these modifications being due to the thickening of the asci.

DISCOID FUNGI-DISCOMYCETES

With such a structure it will manifestly be almost impossible to trace the development of the spore and to set at rest the question of sexuality in reproduction. It has been assumed that there is some form of impregnation in the Discomycetes, either for each individual ascus or for the entire cup. Those who have advocated the impregnation of the asci, affect to see in the paraphyses some representative of the male organs, but in support of this theory there is no evidence. The granular contents at the apices of the paraphyses do not suggest spermatia, but mostly colouring matter which imparts the tone of colour to the disc. Advocates have also been found for the fertilisation of the entire cup in its most initial stage of growth. These profess to have found, especially in Ascobolus furfuraceus and in Pyronema confluens, all that they require to establish sexuality. Woronin¹ in Lachnea pulcherrima (Cr.) claims to have ascertained that the cup derives its origin from a short and flexible tube, thicker than the other branches of the mycelium, and which is soon divided by transverse septa, or partitions, into a series of cells, the successive increase of which finally gives to the whole a torulose and unequal appearance. The body thus formed he called a "vermiform body," since designated a "scolecite" 2 (Fig. 71). He also seems to have convinced himself that there always exists in proximity to this body certain filaments, the short arched or inflexed branches of which, like so many antheridia, rest their anterior extremities, on the uniform cells. This contact seems to communicate to the vermiform body a special vital energy, which is immediately directed towards the production of a somewhat filamentous tissue, on which the hymenium, or disc, is at a later period developed.

Tulasne³ observes that this scolecite can be readily isolated in *Ascobolus furfuraceus*. When the young receptacles are still spherical and white, and have not attained more than one-twentieth of a millimetre in diameter, it is sufficient to compress them slightly in order to rupture them at the summit and expel the scolecite. This occupies the centre of the

¹ De Bary, Beitr. zur Morph. der Pilze, 1866.
² See Fig. 26.
³ Tulasne, Ann. des Sci. Nat., Oct. 1866, p. 211.

little sphere, and is formed of from six to eight cells curved in the form of a comma.

In *Pyronema melaloma* Tulasne states that the scolecite in this species is most certainly a lateral branch of the mycelium.



FIG. 71.-Scolecite. After Kihlman.

This branch is isolated, simple, or forked at a short distance from its base, and in diameter generally exceeding that of the filament which This branch bears it. is soon arched or bent, and often elongated in describing a spiral, the irregular turns of which are lax or compressed. At the same time its interior, at first continuous, becomes divided by transverse septa into

Sometimes this special branch eight or ten or more cells. terminates in a crozier shape, which is involved in the bent part of another crozier which terminates in a neighbouring In other cases the growing branch is connected by filament. its extremity with that of a hooked branch. Of these contacts Tulasne was uncertain whether they were normal or But of the importance of the scolecite he conceived accidental. there was no room for doubt, as being the certain and habitual rudiment of the fertile cup. Inferior cells are produced from the flexuous filaments which creep about its surface, cover and surround it on all sides while joining themselves to each other. At first continuous, then septate, these cells by their union constitute a cellular tissue, which increases little by little until the scolecite is so closely enveloped that only its superior extremity can be seen. These cellular masses attain a considerable volume before the hymenium begins to show itself in a depression of their summit. So long as their smallness permits of their being seen in the field of the microscope, it can be determined that they adhere to a single filament of the mycelium by the base of the scolecite, which remains naked.¹

The same investigator claims to have been more successful in his search after some act of copulation in his experiments As early as 1860 he recognised the with Pyronema confluens. large, globose, sessile, and grouped vesicles which originate the fertile tissue, but did not comprehend the part which they Each of these emits from its summit a were to perform. cylindrical tube, generally flexuous, but always more or less bent in a crozier shape, sometimes attenuated at the extremity. Thus provided, these utricles resemble so many tun-shaped, narrow-necked retorts, filled with a granular, thick, roseate protoplasm. In the middle of these, and from the same filaments, are generated elongated clavate cells, with paler contents, and more vacuoles, termed by him paracysts. These, though produced after the other bodies, or macrocysts, finally exceed them in height, and seem to carry their summit so as to meet the crozier-like prolongations. It would be difficult to determine to which of these two orders of cells belongs the initiative of conjugation. Sometimes the advance seems to be on one side and sometimes on the other. However this may be, the meeting of the extremity of the connecting tube with the summit of the neighbouring paracyst is a constant fact, observed over and over again a hundred times. There is no real junction between the dissimilar cells, except at the very limited point where they meet, and there a circular perforation may be discerned at the end, defined by a round swelling, which is either barely visible or sometimes very decided. Everywhere else the two organs may be contiguous, or more or less near together, but they are free from any adherence what-If the plastic matters contained in the conjugated cells ever. influence one another reciprocally, no notable modification in their appearance results at first. The large appendiculate cell seems, however, to yield to its consort a portion of the plasma One thing only can be affirmed from these it contains. phenomena-that the conjugated cells, especially the larger, wither and empty themselves, while the upright compressed

> ¹ Cooke, Fungi, their Nature, Uses, etc., p. 174. 12

filaments, which will ultimately constitute the asci, increase and multiply.1

Starting with this idea of the general structure of the discoid Fungi, it will scarcely be difficult at any time to distinguish the various genera and species from those of the residue of ascomycetous Fungi. The latest revision of the classification is that by Professor Saccardo, and he has enumerated altogether 3450 species, distributed over twelve families and included under 190 genera.

The most striking divergences from the cup-shaped type are those of the pileate forms, in which, as in Morchella (Fig. 72),



the irregular cups are gregarious upon a common stroma; or in others of the pileate genera in which the hymenium is spread over the upper surface of erect clubs, as in Geoglossum, or expanded laminae, as in Helvella. In all these cases the fructifying surface is superior and exposed, and the sporidia are contained in membranaceous sacs or asci, which latter are not enclosed in closed perithecia. Many of them FIG. 72 .- Morchella esculenta, are large enough and succulent enough

to be employed as articles of food, and

we do not remember that any one species has been proved to be poisonous, although doubts have been expressed of the wholesome character of one or two, and notably of Gyromitra esculenta.

The largest number inhabit the ground or flourish on rotten wood, and by far the most part are confined to temperate climates, species found in tropical or subtropical regions being chiefly those of a tough and leathery consistence. The Morels, for instance, when they occur in India, are found at considerable elevations on the Himalayas, where the climate corresponds to that of temperate regions (Fig. 73). The analogues of the fleshy Pezizae are found under the aspect of Cenangium, Urnula, or Tympanis in warm climates; whilst in Mexico and

¹ Tulasne, "On the Phenomena of Copulation in certain Fungi," Ann. des Sci. Nat., 1866, p. 211.

DISCOID FUNGI-DISCOMYCETES

India a large leathery Fungus of the genus *Midotis* takes the place of the species of *Otidea* found in Europe.

The Fungi in this group which exercise a deleterious influence on growing plants are limited in number, and confined to two or three genera. It has been declared that a

small Peziza, under the name of Peziza Willkommi, is the cause of the devastating larch disease; whereas we are of opinion that it is really the same as Dasyscypha clandestina, and is parasitic upon the diseased spots, caused by resinosis, and is not the source of the disease. More decided, however, are the relations between the small species of *Pseudopeziza* and the living plants which they attack. One of these common on clover, another on is lucerne, and others on Caltha, Galium, All these are undoubtedly deetc.



FIG. 73.—Himalayan morel,' with section and sporidium.

structive, but outside this genus nearly all the leaf-species only occur upon leaves subsequent to death or decay. A very abnormal series of forms, most nearly related to the *Discomycetes*, and classed with them, are the occasion of peach blister, the pear-leaf blister, and similar diseases. These Fungi of the genus *Exoascus* have no proper excipulum, but consist of naked asci, placed side by side on a kind of mycelium investing the blistered spots.

It would be scarcely out of place to allude here to a few species of the form of *Peziza*, but classed together under the generic name of *Sclerotinia*, which are developed from fungoid bodies called *Sclerotia*—which are a sort of compact mycelium —and after a period of rest give rise to species of *Peziza* or *Sclerotinia*. One of these is common on a *Sclerotium* found in company with the roots of the wood anemone (Fig. 74). Another is developed from a little black *Sclerotium* often common in the haulms of potatoes and cabbage-stalks. Another, again, occurs on a *Sclerotium* developed within the substance of rushes. The injury to the plants is caused in the *Sclerotium* stage, but the mature Fungus bears the common name of *Sclerotinia*.

Some mycologists have advanced the opinion that at least many of the species of the genus of moulds named *Botrytis* are the conidia of some species of *Peziza*.

It has been shown by Tulasne, and others, that some of the discoid Fungi appear under two or more forms or phases,



FIG. 74.—Sclerotinia tuberosa on anemone. Gard. Chron.

which resemble each other in outward appearance, but differ in fructification. In the case of Calloria fusarioides, on nettle stems, there is a conidial form in which no asci are developed. but naked spores are produced on sporo-Later on, phores. and upon the same stems, in company with the conidia true cups are perfected which contain asci Both and sporidia. are of the same size and colour, and in well-developed specimens it is difficult to distinguish them without the use of the microscope. In the case of Coryne sarcoides the same resemblance exists between the two con-The form ditions. which conidia in

only are produced was previously called *Tremella sarcoides*, and is of a peculiar reddish-violet colour, bursting in clusters through fissures in wood or bark. The perfect

DISCOID FUNGI-DISCOMYCETES

condition probably exhibits a more definite disc, but the asci are well developed, containing eight sporidia of an elongated form, at first nucleate but ultimately triseptate. In the genus Tympanis it is not unusual to meet with cups which have no asci and only bear stylospores or conidia. The various species of Cyphella are suspicious of relations to Peziza, but not yet satisfactorily determined. The species in this genus are imitations of Peziza in form, but the disc is more like the hymenium of Corticium, and hence the genus is located in the Hymenomycetes. Many of these were called by the name of Peziza before the fructification was investigated, and in the future some of them may have to be restored again as the stylosporous conditions of true Pezizae. There are still to be found, in two groups widely apart, the Clavaria nigrita in the Hymenomycetes and Geoglossum nigritum amongst the Discomycetes, hardly distinguishable in appearance, but bearing in the former case naked spores and in the latter sporidia enclosed in asci.

The relations of the discoid Fungi to other groups has sometimes been matter of speculation. Some of the larger *Pezizae* have a subterranean habit in the first instance, and the cups almost closed, excepting a perforation at the apex; but in *Berggrenia* the species are completely closed and subterranean. In all other respects they are *Pezizae*, the inner walls of the receptacle bearing the asci in the form of a continuous hymenium. Another genus, at present grouped with the *Tuberaceae*,¹ or truffle family, is called *Hydnocystis*, and the structure is so similar that it becomes doubtful whether there is any valid generic difference. At any rate this appears to be the point where the *Tuberaceae* are united to the *Discomycetes*, and whence they diverge.

If the several genera of *Patellaria*, *Patinella*, *Durella*, and *Lecanidion* are compared with such genera as *Lecidia* amongst

¹ Berkeley says: "There is a small group of *Pezizeae* which grow in sand or on loose earth, in which the cups are more or less buried. These species are scarcely distinguishable from *Hydnocystis*. In the species which are more nearly allied to *Peziza*, the asci are often cylindrical, and the sporidia of moderate dimensions." And again : "*Hydnocystis* is, in fact, very near to such Pezizee [*P. sepulta*, etc.], though essentially distinct and far more neat in habit" (*Introduction to Cryptogamic Botany*, p. 286).

the Lichens, it will be observed that here again the discoid Fungi come almost in touch with another outside group, and seem to pass almost insensibly into Lichens, destitute of a visible thallus. Amongst the *Sticteae* there are such genera as *Xylographa*—which some lichenologists still claim, but which mycologists will not reject—in which the relations of Fungi and Lichens are most intimate. In *Platysticta* as compared with *Platygrapha*, and some species of *Stictis* with *Thelotrema*, the resemblance, if not affinity, is maintained.

The classification adopted by Fries in this, as in all other groups, was based primarily on external characters distinguishable by the aid of a common lens. Microscopical characters had none, or but a subsidiary place. Although his success was very great in appreciating affinities, considering the limits of his investigations, yet much was left imperfect and undecided when subsequent observers came to apply the microscope. It was felt that, however great was the success when applied to large objects, the system was not sufficient for small ones; so that, step by step, alterations and additions were proposed by Fuckel, Karsten, and others, which culminated in the carpological system elaborated by Saccardo. Whether, as a whole, this latter is too artificial to satisfy the aspirations of those who believe in natural affinities, must be left to individual judgment. The basis of classification being transferred from external characters to internal fructification, there was a manifest danger lest external characters should be wholly ignored; fortunately, however, this was not the case, so that the result may be expressed as a combination of the two, giving the pre-eminence to the carpological.

The fructification of the discoid Fungi, as compacted in the disc, consists of the asci and their contents and appendages that is to say, the asci and their contained sporidia, and the paraphyses. The asci for the most part are cylindrical, or else clavately cylindrical, seldom ovate or approaching to globose. The sporidia, subject to considerable variation in form and size, are to a greater extent simple and uncoloured than in any other group of Ascomycetes; in the larger species elliptical or globose, in the smaller cylindrical or fusoid—the colour of the sporidia and their septation being held as of generic value. By this means the larger genera have been divided into smaller ones, with analogous external characters, as part of the diagnoses.

The paraphyses are more highly developed, as a rule, than in the Pyrenomycetes. In many the clavate or swollen extremities contain coloured granular protoplasm, which contri-The asci themselves are bute to the colour of the disc. uncoloured, but the paraphyses being very numerous, and exceeding the asci in length, determine the colour of the In some few instances it has been hymenial surface. suspected, rather than proved, that the paraphyses are capable of bearing conidia. In some genera the paraphyses are acute at the tips and thickened downwards, uncoloured, and extending beyond the asci more than usual, so as to impart a minutely velvety appearance to the disc. In certain genera the asci, when mature, are projected beyond the paraphyses and the surface of the disc, and sometimes are expelled with the sporidia within them.

It was thought at one time, and perhaps a few faithful votaries still survive, that the application of iodine to the hymenium would be a valuable aid in the discrimination of species. Most practical men have, however, discarded it after trial, upon the conviction that it is not a trustworthy guide. Reagents may be useful with the denser apothecia of Lichens, but only with such *Pezizae* as are most nearly allied to Lichens in texture.

In comparing the sporidia of the discoid Fungi with those of the Pyrenomycetes it will be observed that, even in cases where the sporidia are coloured, they are few in number and not so opaque; and that as for the form, the most typical in the Discomycetes is the elliptical, and in the Pyrenomycetes the fusiform. The clathrate or muriform spore, not uncommon in *Sphaeriacei*, is almost unknown in the *Pezizei*. Successful artificial culture or germination of spores in the Discomycetes has been accomplished in a few genera.

It seems worse than folly to attribute, as some do, every peculiarity of structure, habit, or coloration to some special purpose, such as protection, attractiveness, etc., without having any basis of fact for their conclusions. There are plenty of

such problems to solve in connection with discoid Fungi, but the facts are few and the inferences are not self-evident. In certain isolated cases they may be, but they concern mostly only the species in question, and are not of general application. Take, for instance, the case of Geopyxis ammophila. Here is a Peziza of considerable size, of the colour of sea-sand, the exterior usually covered with particles of sand, and the base attenuated into a tapering root three times in length that of the cup. When it is known that this species is found only on loose sandy dunes, it is at once concluded that the long rooting base serves a useful purpose in attaching the Fungus well into the loose sand and thus preventing its drifting away to destruction, whilst the inconspicuous colour masks its presence and prevents its being designedly uprooted. But it is not always evident, as in this case, what is the purpose of the peculiarity. The semi-subterranean species of Sepultaria are mostly of some shade of brown, and the exterior is covered with a dense matting of interwoven hairs. They affect a globose form, with the disc but slightly exposed, except when saturated with moisture. Blown away from their attachment, their form assists them in being transported from place to place, until a wet locality is reached, when the cup more or less expands, and they drift no more until again dried and closed, when the globose form is resumed. The colour, approximating that of the soil, may be deemed a protection, and the dense woolly coat a means of retaining moisture, as well as preventing rapid evaporation and consequent desiccation. But that which may be true enough of one species, or of one series of species, is not necessarily a theory of universal application. It is true that nearly all the species of Ascobolus which grow upon dung are so inconspicuous that they can only be distinguished from the matrix by close observation. It might be inferred that this accommodation of colour was intended for the preservation of the individual and the perpetuation of This would not apply, however, to Humaria the species. granulata, which is very common in large patches, of a bright orange colour, on the same matrix, very conspicuous at a considerable distance. In this instance colour can be no protection, but what is the purpose of the bright colour?

DISCOID FUNGI-DISCOMYCETES

Then there is the well-known Peziza aurantia, three inches in diameter, growing amongst grass, several orange species of Humaria scarcely a quarter of an inch in diameter, growing on the naked soil, and in both cases with a smooth external Compare these with the orange or red species of surface. Scutellinia which flourish on wood and have the exterior covered with brown bristles. Does the colour serve the same purpose in all, and, if so, why are the species of Humaria smooth and those of *Scutellinia* covered with bristles? These are problems not easily solved, because the substratum of fact is imperfect. It will not serve to assume that the bright colour is an attraction to insects, since it is not known that the visits of insects would be of much service to the Fungus. If there is no known process of fecundation there will be no cross fertilisation to accomplish, and the dispersion of the sporidia is assured by the elasticity of the asci and the force with which the sporidia are seen to be expelled in a little cloud, puffed out at intervals under the influence of sunlight. It would be folly to dogmatise, and say that coloration of the disc is only accidental, and of no service to the plant, because observation has as yet given no clue to the mystery. It would be far more reasonable to assume that there is a purpose for everything, and endeavour to ascertain what that purpose may be. Why are the majority of brightly coloured species of a soft and fleshy consistency, as in Calloria and Orbilia, and why are the black, or nearly black, species tough and coriaceous, as in Tympanis and Urnula?

The economic uses of the discoid Fungi are limited to but a few species, and these comprised within three or four genera. The Morels are widely known and appreciated, and deserve to stand at the head of the list. There are in all twenty-four species of *Morchella*, all of which may be assumed to be edible. Eighteen of these are European, two North American, two Asiatic, one common to Russia and North America, and one confined to the Canaries. Two or three of the European species have a wide distribution, being found also in North America, Australia, Tasmania, and Kashmir. The nine species of *Gyromitra* are rarer and of less importance. *Helvella*, though including forty-five species, contain a large proportion which

are too small for practical use. The two best known and appreciated are the European *Helvella crispa* and *Helvella lacunosa*.



FIG. 75.—Cyttaria, with section.

Corresponding to the true Morels are the seven species of Treemorels (*Cyttaria*) (Fig. 75), which grow on the trunks of various species of birch in the Southern Hemisphere, Chili, Tierra del Fuego, or Fuegia,

Tasmania, and New Zealand. In Fuegia they are so important as to constitute the staple food of the Fuegians during many months of the year. In appearance they somewhat resemble the Morels, but are rather more gelatinous and smaller. "Where Fungi form a large portion of the food of the people, it is in general a sure indication of

an unproductive climate or an extremely depressed peasantry; but it is possible that the qualities of *Cyttaria* (Fig. 76) may be superior to those of other Fungi, arising probably from its immediate imbibition of the elaborated gummy sap of the matrix."¹ The other esculents remaining are



FIG. 76.—Beech Morel, Cyttaria Gunnii, with section.

nearly all the larger species of *Peziza* or *Discina*, which are more or less eaten throughout Europe, but have very little to recommend them. *Discina venosa* is sometimes sold under the name of Morel.

All the collections of Fungi hitherto made in tropical countries have exhibited a preponderance of the large woody species of *Fomes* and other *Polyporei*, which are not only persistent through the year, but are also of a size readily to be seen by the collector, and giving but little trouble in their preservation. On this account the minute and inconspicuous species

¹ Berkeley, Introduction, p. 293.

DISCOID FUNGI-DISCOMYCETES

have been overlooked, so that the catalogues of Fungi from the tropics are always to be suspected as very incomplete in their enumeration of the Ascomycetes, except in a few instances where a competent resident has superintended the investigation. Hence a comparison of the species recorded from such places with those found in Europe is hardly just to the tropics, and would not, at present, offer a fair estimate of geographical distribution. Out of a total of about 1200 species collected in Ceylon by Dr. Thwaites there were fifty discoid Fungi and upwards of 200 Sphaeriacei. This is a much larger proportion than usual, but in neither case can it be regarded Taking the whole estimate of described as exhaustive. Hymenomycetal Fungi at 9000, those of the Discoid Fungi, for all the world, are upwards of one-third of that number, and of Sphaeriacei two-thirds more; so that the proportion for Ceylon, with 700 Hymenomycetes, would have been some 230 Discomycetes and upwards of 450 Sphaeriacei. Hence to bring up the proportion to the universal ratio there should have been nearly five times as many Discomycetes, and more than twice as many Pyrenomycetes, found in Ceylon. If this does not indicate that the Discoid Fungi are one-fifth less in number in the tropics than in an universal total, then the only conclusion remaining is that the list of Ceylon Discomycetes is still incomplete, and yet Ceylon has been one of the most favoured localities in having Dr. Thwaites as a resident. In other tropical countries there is a still greater disparity, so that it would be premature to draw inferences of geographical distribution based upon present knowledge.

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CHAPTER XVI

SUBTERRANEAN FUNGI-TUBERACEAE

Two very similar small groups of Fungi resemble each other very much in habit and in external appearance, but differ considerably in their internal structure. These are the somewhat globose balls which are produced under the surface of the soil, and called Tuberaceous or Subterranean Fungi. One group has the spores developed in asci, belonging therefore to the *Ascomycetes*, and the other has the spores naked on basidia, and so belong to the *Basidiomycetes*, or that section called *Gastromycetes*. The former are represented by the true Truffles, and the latter by the false Truffles or *Hypogaei*.

To begin with the simplest forms, we encounter structures which resemble small underground species of *Scleroderma*.

They are mostly somewhat globose in form, of a dirty colour, with a thick outer coat or peridium. In one or two genera the outer coat is thin or obsolete; when mature, if cut through the centre, they are seen to be filled with a powdery mass of dark-coloured spores, but if cut when young the interior is streaked and mottled, at length full of small cavities, in which the spores are produced. The spores themselves are sometimes elliptical or almond-shaped, with either a rough



Spores of Octaviana.

or smooth surface, or they are globose and warted (Fig. 77). It may well be said that these Fungi are underground puff-balls, which are united to the terrestrial *Gastromycetes* through the species of *Scleroderma*, one of which has often a modified subterranean habit. In former times a species of *Melanogaster* was sold and used, under the name of Red

Truffle, as a substitute for the genuine article (Fig. 78). Many of the species possess a strong penetrating odour, which may be useful in guiding animals where to search for them, but can scarcely be protective. From their habit they are very difficult to find, and hence are regarded as more uncommon than



FIG. 78.—Section of Melanogaster.

they probably are. They seem to prefer a sandy soil, and are to be sought near the roots of trees. Altogether not more than seventy-five species are known, of which no less than sixty are European. A very few occur in Australia, about fifteen in America, one or two in Africa, and about three in Asia, so that it is pre-eminently a European group. Whether we regard them as degenerate Truffles or sub-

terranean puff-balls, they appear to be the link which unites the *Basidiomycetes* to the *Ascomycetes*, by means of the *Tuberacei* or genuine Truffles. In old age, when the asci are dissolved, it is difficult to distinguish the species of *Elaphomyces* from the *Hypogaei*.

In their earlier stage it is not difficult to determine the character of the fructification. Then the walls of the internal cavities are lined with basidia or elongated cells, crowned at the apex with two or four little spicules or sterigmata, at the tips of which the spores are produced. When mature the spores fall away, and lie free in the cavities. From the number of spores that these cavities contain, the Rev. M. J. Berkeley was led to infer that spores were produced consecutively; but there is no substantial evidence to support this view, and no analogy in any other group of *Basidiomycetes*, so that we fear the theory is untenable.

Of the germination of the spores, the production of mycelium, and gradual development of the young plant, we are not aware that anything positive is known; and the Fungi themselves being of no economic value, their cultivation has not been attempted.

From the Gastromycetal *Hypogaei* we turn to the more highly developed *Tuberacei*, and here we find in most cases

SUBTERRANEAN FUNGI-TUBERACEAE

that the individuals attain a far larger size and a greater value, from the utilitarian point of view. The interior does not become pulverulent in the genuine Truffles, although it does in Elaphomyces, and when cut through in section the flesh is mottled and veined. Slices of the substance under the microscope exhibit rounded delicate sacs or asci, which enclose the sporidia lying freely within them. Externally the surface of the peridium is often warted or rough, and the resemblance to a subterranean Scleroderma is more remote. The total number of described species scarcely exceeds one hundred and twenty, of which fifty belong to the genus Tuber, and all except eight are European. Of the extra-European species two belong to Ceylon,¹ one to Malacca, one to North America, three to South America, and one to Tasmania. It is somewhat remarkable that North America is so deficient in examples of this group, as only two or three of the European species have been found there in addition to the one indigenous species. The species of Mylitta, or native bread, are not genuine members of this group, although often associated with them, but they would seem to belong rather to that congeries of imperfect forms termed Sclerotia.

The most prolific country for the production of species of Truffles is Italy, but the most celebrated of Truffles for the table are those of France. At one time Truffle hunting was conducted with success in the southern coun-

ties of England, but for many years the industry has declined, and is now almost extinguished. This is said to be due to the importation of French Truffles of more exquisite flavour, and

at a lower price. All Truffle spores are large, FIG. 79. - Alveothose of our common British species being alveolate, or covered with hexagonal pits, the



late sporidium of Truffle.

walls of which are of transparent membrane (Fig. 79). The spores of the French Truffles are spinulose (Fig. 80). It is easy, by aid of the microscope, to determine even by a fragment the French from the English Truffle, or Tuber aestivum from Tuber melanosporum, on account of the difference in the sporidia. "The extent of the trade in Truffles may be estimated from the fact

¹ Some kind of Truffles are reported to be found in the Kangra Valley, India.

that in Apt upwards of four thousand pounds are sold every week during the height of the season, whilst the department



FIG. 80.-Spinulose sporidium of Truffle.

of Vaucluse yields about thirty tons per annum." Berkeley says that "though a few species are not confined to limestone formations, it may be assumed in general that Truffles require a calcareous soil for their growth, and that they increase in number of species and individuals as we approach the southern limits of our island. And if this is true of Truffles in general, it is more especially so the esculent kinds, which are alone likely to be

as regards the esculent kinds, which are alone likely to be objects of cultivation."

The problem of Truffle cultivation has been discussed over and over again, and experiments have been made, with more or less success. MM. Tulasne have shown that an abundant spawn is produced in several genera. The common Truffle exhibits in the soil in which it grows, during the month of September, a profuse mycelium of white cylindrical strings, more slender than sewing-thread, which themselves consist of multitudes of delicate articulated filaments, communicating with a kind of byssoid mass, some lines in thickness, surrounding the young Truffles. This mass soon disappears, so that only a few isolated filaments remain attached to the surface of the Truffle.

Attempts have been made from time to time to propagate Truffles, or to produce a saleable spawn, but hitherto with but small results. In the south of France one nobleman succeeded in raising Truffles in his woods by sprinkling the soil with water in which the parings of Truffles had been rubbed down, and protecting the ground.

Some trees appear to be more favourable to the production of Truffles than others. Oak and hornbeam are especially mentioned, but besides these chestnut, birch, box, and hazel are alluded to. The old Truffle hunters obtained them chiefly under beech, and in mixed plantations of fir and beech.

Count de Borch and M. Bornholz wrote the chief accounts of Truffle culture. "They inform us that a compost was prepared of pure mould and vegetable soil, mixed with dry leaves and sawdust, in which, when properly moistened, mature Truffles

SUBTERRANEAN FUNGI-TUBERACEAE

were placed in winter, either whole or in fragments, and that after a lapse of time small Truffles were found in the compost. But the result was discouraging rather than otherwise. The most successful plan consisted in sowing acorns over a considerable extent of land of a calcareous nature; and when the young oaks had attained the age of ten or twelve years, Truffles were found in the intervals between the trees. This process was carried on in the neighbourhood of Loudun, where Truffle beds had formerly existed, but where they had long ceased to be productive-a fact indicating the aptitude of the soil for the purpose. In this case no attempt was made to produce Truffles by placing ripe specimens in the earth; but they sprang up of themselves from spores probably contained The young trees were left rather wide apart, and in the soil. were cut for the first time about the twelfth year from the sowing, and afterwards at intervals of from seven to nine years. Truffles were thus obtained for a period of from twenty-five to thirty years, after which the plantations ceased to be productive, owing, it is said, to the ground being too much shaded by the branches of the young trees—a remedy for which might have been found by thinning out the trees, but this would not be adopted till all the barren tracks had been planted. The brushwood by being thus thinned out would be converted into timber trees; and the Truffle grounds rendered permanent, like those of Poitou, which are commonly situated under the shade of lofty trees. It is the opinion of MM. Tulasne that the regular cultivation of the Truffle in gardens can never be so successful as this so-called indirect culture at Loudun; but they think that a satisfactory result might be obtained in suitable soils by planting fragments of mature Truffles in wooded localities, taking care that the other conditions of the spots selected should be analogous to those of the regular Truffle grounds; and they recommend a judicious thinning of the trees, and clearing the surface of brushwood, etc., which prevents at once the beneficial effects of rain and of the direct sun rays. It is added that this species of industry has added much to the value of certain districts of Loudun and Civray, which were previously comparatively worthless, and has enriched many of its proprietors, who now make periodical sowings of acorns,

13

thus bringing in a certain portion of wood as Truffle grounds each year. At Bouardeline, for instance, the annual return from Truffles in a plantation of less than half an acre was from $\pounds 4$ to $\pounds 5$. Another case is adduced in the arrondissement of Apt, where several proprietors have made plantations; the trees are left about five or six yards apart, and so soon as their branches meet, and shade the ground too much, they are thinned out."¹

There are several other genera of Tuberaceous Fungi, but of little or no commercial importance. The species of



FIG. 81.—Hydnotrya Tulasnei.

Hydnotrya (Fig. 81) have long twisting cavities in the interior, and the sporidia are globose and warted. In Hydnobolites the sporidia are globose and alveolate (Fig. 82). In Choiromyces the sporidia are also globose, covered

with blunt spines. These Tubers sometimes attain to the size of a man's fist. The African Truffle is *Terfezia leonis*, which was discovered about four hundred years ago. For ages Truffles have been eaten by the natives, but a peculiar interest attaches

to this species from the fact that the French Academy of Sciences recently discussed them; and it is probably this species of which it is said that they can be imported from Bagdad and Biskra

so that they can be sold in the markets of Paris at about one penny per pound.



FIG. 82.—Hydnobolites with sporidium.

This is possibly an exaggeration, but at six times the price they would have some influence on the Truffle trade. One species is reported to realise twelve shillings a pound in Italy, but what a comparison !

In the genus *Sphaerosoma* the hymenium soon becomes exposed (Fig. 83), the elongated cells or asci are closely packed together side by side, as in the species of *Peziza*; so that the genus approaches the character of a subterranean Discomycete, as also does another genus named *Hydnocystis*. Indeed, it is difficult to distinguish this genus from *Berggrenia*, which is

¹ C. E. Broome in Journ. Roy. Hort. Society, and in Gardener's Chronicle, 21st. Oct. 1865.

SUBTERRANEAN FUNGI-TUBERACEAE

classed under the Discomycetes, and may possibly be the same genus with another name. At any rate the *Tuberacei* are joined to the Discomycetes by these genera, which form the connecting link, and they might almost as well be regarded as aberrant *Pezizae* as abnormal Tubers.

One of the largest genera of *Tuberaceae*, next to the genuine Truffles, is *Elaphomyces*, with its

twenty-one species (Fig. 84). The interior mass soon becomes dusty and black, like soot, caused by the



the cavities and the asci which at and spores. first enclose the sporidia (Fig. 85), leaving only the free, darkcoloured spores to constitute the internal dust. We collected



FIG. 84.-Elaphomyces and section.

four or five species on one occasion, in a young chestnut wood at Montmorency. All the known species are European, and only one or two of these have been recorded out of Europe. Most of them are nearly globose, and the

outer coat is harder than in the Truffles. In former times they had a fanciful reputation in medicine, but have long since gone out of use.

It will be observed that in the majority of the *Tuberaceae*, where the pressure is equalised during growth, the asci, which

contain the sporidia, approach a globose form, whilst in the genera where the hymenium is effused over the interior, as in those which approach the Discomycetes, the pressure is lateral and the asci assume a cylindrical form, as typical in the fleshy Discomycetes. In none of them are paraphyses present. No facts are known which can lead to



FIG. 85. — Sporidia of *Elaphomyces*.

the inference that any kind of sexual reproduction is probable in this group; and although it is believed that the germination of the sporidia results in the production of mycelium, but little is known of the process of germination. Spores, or sporidia, consisting of a single cell appear to be universal, and the form approaches more nearly to the globose than any other.

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CHAPTER XVII

CAPSULAR FUNGI-PYRENOMYCETES

ADVERTING to what has already been written of the Ascomyceteae, it will be remembered that the largest and most important group of those there enumerated is that of the Pyrenomycetes, although, perhaps, the Discomycetes may be considered as the most highly developed. It may be premised that the total of described species for the whole world, up to date, is not less than 10,500, or not less than one thousand more than the whole known Hymenomycetes. The first distinct recognition of the Pyrenomycetes by Fries was in 1849, and then it was supposed to include not only the Sphaeriacei and the Perisporiacei, but also the Sphaeropsidei and Melanconiaceae. In more recent times, when ascigerous Fungi were separated from stylosporous Fungi, the Pyrenomycetes were revised, and the ascigerous species only retained as a portion of the Ascomycetes. With this limitation they are included in Saccardo's Sylloge and universally accepted. Reduced to its simplest designation, the Pyrenomycetes are ascigerous Fungi, having the fructification enclosed within a perithecium, and growing on vegetable or animal substances, but are never truly terrestrial. The various families depend for their most prominent feature upon the character of this perithecium. The form varies within definite limits, as well as the texture and the mode of dehiscence. Normally the form is spherical, or nearly so, and minute, seldom much larger than a good-sized pin's head, and either with or without a more or less elongated neck, not unlike a miniature flask. This may be entirely immersed, or absolutely superficial, or intermediate. The texture may be membranaceous or fleshy, and then brightly coloured; or tough and

coriaceous, or hard and carbonaceous, and usually black. Dehiscence may take place by means of an apical pore or mouth, occasionally elongated but more commonly circular and dot-like; or the perithecium may be absolutely closed, and



when mature, splitting irregularly. In all cases the rupture only takes place at maturity, to permit of the escape of the sporidia. As to habit, in some species the individuals are absolutely isolated and *simple*,

FIG. 86.—Perithecium and section.

and either scattered or gregarious; whilst in others they are collected upon a pulvinate, or more or less strongly developed stroma, which may be of variable form and magnitude, and in this condition are characterised as *compound*. The large majority are saprophytic, but a few are parasitic, and the former occur most commonly on dead or decaying wood, branches, twigs, fruits, leaves, or the dead parts of herbaceous plants; the latter are mostly confined to living leaves, or the green parts of growing plants. Other details will follow more conveniently under the several families.

The Perisporiaceae may occupy the first place, in that they are entirely simple, or with the perithecia separate from each other, and not combined in a common stroma; sometimes membranaceous, at others coriaceous or tough, or more rarely hard and brittle; but their most distinguishing feature consists in the wholly closed, or astomous, perithecia, which are irregularly split when mature to permit of the escape of the sporidia. It will be most convenient to review the details under the several subfamilies, the first of which, at least, is a compact and natural group. The Erysipheae are of parasitical habit, and flourish on the living leaves and green parts of arborescent and herbaceous plants. In the first instance a web-like mycelium effuses itself broadly over the parts attacked, and in this condition the leaves assume a white and mouldy or chalky appearance, as if powdered with flour. In this stage the delicate threads of mycelium, like a spider's web, interlace each other, are repeatedly branched, and adhere closely to the surface by the means of haustoria or suckers. From this mycelium arise erect fertile branches, which become differen-

CAPSULAR FUNGI-PYRENOMYCETES

tiated into chains of hyaline conidia, which fall away and are capable of germinating and producing a new mycelium. In

this condition the parasite is a mould, or Hyphomycete, and was formerly included under the genus Oidium, under the supposition that it was a complete and autonomous Fungus. Recent investigation has shown that this stage of mould is only the conidial condition of FIG. 87. - Perithecium and some species of the Erysipheae, which succeed the Oidium. In the first in-



ascus with sporidia of Erysiphe.

stance minute spherical yellow bodies appear on the surface of the mycelium, and these gradually enlarge until they become just visible to the naked eye, and acquire a dark brown colour



FIG. 88.-Uncinula.

(Fig. 87). These are the perithecia, or membranaceous capsules, attached at the base by a copious mycelium and surrounded by a circlet of free arms, or processes, as appendages, which vary in the different genera. In Erysiphe they are thread-like and flexuous, of equal diameter throughout, and simple. In Uncinula the arms are hooked or curved at the tips (Fig. 88). In

Phyllactinia the appendages are straight, and often inflated at the base. In Sphaerotheca they are flexuous and sometimes

vaguely branched. In Podosphaera the appendages are repeatedly forked at the tips, as they are also in Microsphaera (Fig. 89). Internally these globose perithecia are replete with the ascigerous fructification. The asci are nearly globose, or pear-shaped, and contain hyaline elliptic sporidia. In Podosphaera and Sphaerotheca each perithecium encloses but a single ascus. In the other



FIG. 89.-Microsphaera.

genera the asci are numerous in each perithecium. The number of sporidia in each ascus varies with the genera, but with the exception of a single genus these sporidia are ovoid and continuous. In the exceptional genus Saccardia
the sporidia are septate in both directions. In all cases these Fungi are destructive pests, by choking the pores or stomata, although only flourishing on the external surface. Such are the rose mildew, *Sphaerotheca pannosa*; the hop mildew, *Sphaerotheca castagnei*; the pea mildew, *Erysiphe Martii*, and others. The number of known species is about 100.

The next subfamily, Perisporieae, is more numerous, and whereas the majority of the Erysipheae are confined to cool and temperate regions, the majority of the Perisporieae are sub-The species are not parasitical, or to a limited extent, tropical. and the subiculum, when present, may be either colourless or coloured, mostly the latter. The perithecia, although most commonly subglobose, are sometimes depressed and lens-shaped, and, except in Meliola and one or two smaller genera, without The sporidia are more variable than in the first appendages. subfamily, and hence fall under five sections : Hyalosporae, with continuous hyaline sporidia; Phaeosporae, with continuous coloured sporidia; Didymosporae, with uniseptate sporidia; Phragmosporae, with multiseptate sporidia; and Dictyosporae, with muriform sporidia. Under these various sections the twentyfive genera are distributed. This arrangement foreshadows the principles upon which the several groups of Pyrenomycetes are grouped; that is to say, primarily on the basis of the sporidia, whether coloured or hyaline, and whether continuous or septate. It is unnecessary to occupy space by a synopsis or comparison of the component genera, but simply to make reference to two or three of the most important. Asterina, in its broadest sense, is characterised by a flattened or lens-shaped perithecium, seated on a dark radiating subiculum, with sporidia continuous or septate, hyaline or coloured; hence the principle adopted almost universally by Saccardo, in other genera, of making spore-characters of generic value is set aside, and only employed for the distinction of subgenera. We have always contended in favour of the Friesian system of adopting external characters in the definition of genera, reserving carpological features for subsidiary sections; and hence the genus Asterina, as it finds a place in Saccardo's Sylloge, will serve as an illustration of our method, but not of that of Saccardo, to which it does not conform, and would only do so by elevating the separate

sections to the rank of genera, and distributing them over the Hyalosporae, Phaeosporae, Didymosporae. That is to say, we have advocated the negation of carpological characters as of primary generic importance in favour of their adoption in subsidiary classification. Dimerosporium differs from Asterina in possessing a globose, and not a flattened perithecium, whereas the fructification follows the Asterina type. Another important genus of the Perisporieae is Meliola, which to a certain extent is the analogue of some of the genera of the Erysipheae : (1) by the possession of an effused mycelium, or conidia-bearing subiculum, but in this genus more strongly developed, and of the nature of black moulds, or Dematicae, and not of the Mucedineae; (2) by the presence of appendages surrounding the perithecia; and (3) sometimes by their parasitic habit on living leaves,-differing, however, in the fructification, inasmuch as the sporidia are normally large, septate, and coloured. The genus Perisporium has elongated triseptate sporidia, which break up freely at the joints into the component cells. In this respect there is analogy to a genus of Sphaeriaceae, that of

Sporormia, which latter, except for its perithecia having a distinct mouth, might be allied with Perisporium. It may be stated in general terms that the Perisporieae includes all the Perisporiaceae which do not fall into the first subfamily, that of the Erysipheae; for the third subfamily, that of the Capnodieae, includes only two aberrant genera which have little definite alliance with the Perisporiaceae. The genus Capnodium is distinguished by elongated large perithecia, which are often branched, and usually opening at the apex with a large fringed orifice (Fig. 90). These are seated upon and amongst a dense subiculum of closely jointed or moniliform black hyphae, so as to form



FIG. 90.—Perithecia of Capnodium, with sporidia.

large velvety patches, and are possibly, in some instances, the more complete developments of moulds belonging to the genus *Fumago.* Scorias is allied to Capnodium, but thicker and more spongy, and the perithecia somewhat clavate. Asci tetrasporous,

and sporidia triseptate. The genus Antennaria is more like a dense black mould with moniliform hyphae and apparently minute perithecia, but the fructification is obscure, and hence its true place and position is uncertain. The whole family of *Perisporiaceae* contains about 700 species, and is an outside group of *Pyrenomyceteae*, joining the *Hyphomyceteae* on the one hand with the *Sphaeriaceae* on the other.

The next family to be noticed is the Hypocreaceae, in itself characteristic and distinct, in which most of the typical features, of the Pyrenomyceteae prevail, such as the ostiolate perithecium and ascigerous fructification, but characterised specially by the fleshy, or nearly fleshy, perithecia, usually pale or bright coloured, but never carbonaceous. The stroma, when present, is soft and between fleshy and waxy, rarely forming a subiculum. Sporidia for the most part hyaline. Without indulging in too great prolixity of detail, it may be observed that in our arrangement,¹ which is mainly a regrouping of Saccardo's genera by external characters, we have recognised three subfamilies. In one of these, Hypocreoideae, the species are composite, viz. seated upon or immersed in a stroma. In the second, Nectrieae, the species are simple, viz. the perithecia are distinct from each other, although sometimes densely caespitose. And in the third, Pseudonectrieae, the perithecia are soft and



FIG. 91.-Claviceps on ergot.

membranaceous, or rostrate or elongated, or clavate, sometimes becoming horny, either whitish or dark coloured, and in fact verging on *Sphaeriaceae*. The most highly developed forms in the *Hypocreoideae* are *Claviceps* (Fig. 91) and *Cordyceps*, in which the species assume a clavate or capitate form, and the perithecia are crowded on the upper portion

of a fleshy stroma (Fig. 92). Many of these are found on dead insects, and their conidial forms were formerly known as species of *Isaria*, a genus of Hyphomycetes. These are succeeded by

¹ "Synopsis Pyrenomycetum," by M. C. Cooke in Grevillea.

smaller genera, and at length by Hypocrea, in which the stroma is pulvinate or effused, except in a few species with a vertical

stroma, and the sporidia are formed from a pair of opposed globose cells, which separate at maturity, and then appear to be sixteen globose sporidia (Fig. 93). This is the typical form, but the sporidia vary in most of the subgenera. There can be no doubt that the eight divisions, which are called genera by Saccardo, and separated widely from each other in his system, on account of differences in fructification, are naturally closely allied to each other in structure, habit, and development. The fundamental problem is whether the latter are to be accepted as evidences of close affinity, or the former; and herein we are at issue with Saccardo, contending that his car- FIG. 92 .- Corpological classification of the Ascomyceteae, as developed in the Sylloge, is artificial, whilst



dyceps on pupa.

the method we have adopted is natural. It may be true that an artificial and mechanical arrangement offers greater facilities for the novice or the superficial student, but it fails to satisfy all those who are seeking something higher than a catalogue of Latin names.

In the second subfamily, the Nectricae, the perithecia are all free of each other, sometimes scattered and sometimes



FIG. 93.-Hypocrea, with section and sporidia.

caespitose. The old genus Nectria, as recognised by Fries, included both the caespitose species, which are analogous to Cucurbitaria in habit; and the scattered species, which are analogous to the denudatae group of superficial Sphaeriaceae. In our arrangement the caespitose species are combined under the old name of Nectria, whilst the scattered species find their place in another genus, under the name of Dialonectria. We need not repeat that

under each of these genera modifications of the sporidia fall into place as subgenera. As a matter of fact it is well known

that some of the species of *Nectria* have an early stage in which the stroma develops only conidia without perithecia, and that these conidial forms were in earlier times regarded as autonomous moulds of the genus *Tubercularia*.¹ Later on perithecia appear upon the old stroma, which contain asci and sporidia (Fig. 94).

There are a few species which resemble, when mature, in external appearance certain species of *Nectria* or *Dialonectria*,



FIG. 94.—D, Tubercularia with Nectria; E, Nectria; perithecia seated upon F, section of stroma; G, asci and sporidia. a more or less byssoid Gard. Chron.

but are accompanied capitate conidial by forms which are not to be distinguished from species of the Hyphomycetal genus Stilbum. Such species of the Nectrieae are associated under the genus Sphaerostilbe. Other species, formerly united with Nectria, have the perithecia seated upon subiculum; these are

now separated from that genus, and united under the name of Byssonectria, analogous to the Byssosphaeria of the Sphaeriaceae. In another group, the perithecia, which resemble Nectria, are densely gregarious, and often partially immersed in a velvety subiculum, transformed from the tissues of decaying Fungi. This genus is Hypomyces, each species of which has also a conidial form, which precedes the ascigerous, and corresponds to some genus of the Mucedineae. Some of the species of Nectria and Dialonectria also have conidial forms, which would be referable to the Hyphomycetal genus Fusarium. In these instances we must recognise the relationship between the Hyphomyceteae and the Ascomyceteae, but it would be assuming too much to infer, from a few examples, that all the species of Stilbum are conidia of Sphaerostilbe, or Tubercularia of Nectria, Isaria of Cordyceps,

¹ See Gardener's Chronicle, 28th Jan. 1871.

or various species of *Mucedineae* of *Hypomyces*. The genus *Lasionectria* includes such species of *Nectria* as possess a hairy perithecium, and in this way are analogous to the Sphaeriaceous genus *Venturia* or the section *Villosae* of the old genus *Sphaeria* of Fries. *Gibberella* closely resembles *Cucurbitaria* in habit, but the perithecia, although dark, are waxy, and blue or violet. *Hyponectria* again includes species of the old genus *Nectria*, but the perithecia are immersed in the matrix.

The third subfamily is Pseudonectrieae, and, as the name indicates, links the Nectrioideae with the Sphaeriaceae. The substance of the perithecia is not of the fleshy or waxy consistence of the first two families, but either membranaceous or becoming horny, and not carbonaceous. The genus Melanospora is somewhat analogous to Ceratostoma, the perithecia furnished in most cases with an elongated beak-like rostrum and brown sporidia. Another genus, Acrospermum, is placed by Saccardo in Hysteriaceae, but Fries included it in Sphaeropsideae through ignorance of the fructification. The species are small, blackish, and of a club shape, with no pore at the apex, otherwise analogous to Pocillum, amongst the Discomycetes, and with similar long thread-like sporidia. Two or three other small genera of little importance make up the total of this subfamily and close the Hypocreaceae.

The remaining families of the *Pyrenomyceteae* have in past times been known as the *Sphaeriaceae*, but we prefer to treat them as two large groups, each containing several families. The *Compositae*, in which either a few or a great number of perithecia are collected together upon, or immersed in, a common stroma; and the *Simplices*, in which the perithecia are distinct from each other, and either clustered together or scattered. Normally the colour is black, the substance membranaceous, or carbonaceous, and dehiscence takes place through an apical pore or ostiolum. Fries classified them entirely according to the external features of the perithecia or stroma, and independently of the fructification. Saccardo classified them primarily according to the fructification, and secondarily, in great part, from external features, or these in combination with the sporidia.

The Compositae, or Compound Sphaeriaceae, contain the

following families :- Xylarieae, Dothideaceae, Melogrammeae. Diatrypeae, Valseae, and Eutypeae.

The Xylaricae possess a very definite stroma, which is



FIG. 95.-Stroma of Xylaria, section of with sporidia.

either vertical, or pulvinate, or effused; the perithecia carbonaceous and somewhat immersed, and the sporidia coloured brown and Xylaria is the typical genus, unicellular. with an erect, branched, clavate, capitate, or subglobose stroma, which is white and corky within, and usually solid (Fig. 95). The perithecia are peripherical, and immersed entirely, or partially, in the upper portion of the stroma, on all sides leaving the stem This stem, sometimes very short, sterile. sometimes very long, may be smooth or hairy, but it is always surmounted by a fertile head, dotted with the ostiola of the circumambient perithecia. In some species the entire fungus scarcely exceeds one-eighth of an inch in length, in others it attains to six inches or more, with a diameter as variable; and yet portion and ascus throughout nearly two hundred species the essentials are the same - an erect poly-

morphous stroma, white and corky within, and a peripherical series of immersed, or semi-immersed, perithecia, enclosing brown continuous or unicellular sporidia. At first, and before the perithecia are fully formed, the apex of the stroma is usually pruinose, with pulverulent minute colourless conidia. The species, with few exceptions, grow on rotten wood, in damp situations, in almost all the countries of the world, wherever a timber tree can flourish and decay. In Thamnomyces the stroma is reduced to long black threads, upon which the perithecia are clustered or scattered. In Rhopalopsis the clubs are densely caespitose, with a short stem, or crowded upon a very much branched common stroma. In Poronia the stroma is almost pezizaeform (Fig. 96), with the perithecia immersed in the disc, whilst in Camillea the stroma is subcylindrical and truncate, with the perithecia vertically immersed about the apex. In Daldinia the stroma is sub-

globose (Fig. 97), concentrically zoned within, and the perithecia immersed at the periphery. In Ustulina the stroma is pulvinate,

becoming hollow; and in Nummularia discoid, and plane or concave, distinctly margined. But in the large genus Hypoxylon, the stroma is either subglobose (Fig. 98) or effused, solid and dark within, closely adnate, of variable thickness, sometimes reduced to little more than a crust of densely-packed perithecia. All these genera are allied by the possession of a stroma and unicellular brown sporidia, as well as their habit of growing upon decayed wood and dead branches, with the exception of Poronia, most of which flourish upon old dung.



section (enlarged). Gard. Chron.

species of Hypoxylon, but differ in the perithecia being formed from the stroma; or, in other words, are fertile cavities excavated in the stroma, without definite ostiola. There are three subfamilies, viz. Dothideoideae, Rhytismoideae, and Stigmatoideae. In Dothideoideae and Rhytismoideae the species are compound, and in Dothideoideae the carbonaceous or coriaceous stroma is seldom broadly effused, and the pseudo-perithecia dehisce when mature by an apical pore. The largest genus is Phyllachora, in which the stroma is either shield-like or shortly effused and superficial, and the species are most commonly found growing on leaves, and not rarely whilst they are still living, but sometimes when dead. The sporidia are uncoloured and unicellular in typical forms, but in some of the subgenera they are coloured and continuous, or uniseptate, and in others uniseptate and hyaline, but rarely triseptate and hyaline or coloured. In Dothidea the stroma is erumpent and pulvinate, the sporidia again are variable, according to the subgenera. The species occur, in most cases, on branches, and rarely on leaves, in which feature it differs from Phyllachora. In

Euryachora the stroma is broadly effused and punctulate, whilst in *Homostegia* the stroma is plane or hemispherical, and the



FIG. 97.—Daldinia, globose stroma and section. Gard. Chron.

species are parasitic upon Lichens. In Rhopographus the stroma is elongated and linear, suggesting a resemblance to some Hysteriaceous perithecia. Species of Phyllachora are common on coriaceous leaves in tropical counand are sometimes tries. difficult to distinguish at first from some of the Rhytismoideae. In common with the latter the stroma is often present for some time before the fructification is developed, hence they are often met with in a sterile condition.

The subfamily *Rhytis*moideae is included by some on account of the mode of

authors with the *Discomyceteae*, on account of the mode of dehiscence, which is usually by gaping fissures, so that the hymenium is more or less exposed; but this dehiscence does

not take place until the sporidia are fully mature, and sometimes not until disintegration has commenced. In external appearance the species are very similar to *Phyllachora* and *Euryachora*, and yet in texture of the stroma, and often in the fructification, appear to be more closely allied to the *Dothideaceae* than to any family of the *Discomyceteae*. Practically, the only genus is *Rhytisma*, for the sporidia of so many described species are unknown that no proposals have been



FIG. 98.—Globose stroma of *Hypoxylon*, with asci and sporidia.

possible to divide them into genera based upon the fructification. Such a species as *Rhytisma acerinum*, which is common on the living leaves of maple, belongs to the Sphaeropsideae in that condition, but after resting on the ground during the winter, asci and sporidia are developed.

The third subfamily, Stigmatoideae, includes genera in which the perithecia are distinct from each other, and therefore divergent from the family type, and approaching the Superficiales of the old genus Sphaeria. Hypospila has, however, a feature which associates it with Dothideoideae, in the definite stroma in which the perithecia are immersed; and also, on this account, Trabutia shows a relationship with Phyllachora. In the genera Stigmatea and Parodiella the perithecia are superficial and globose, often found growing on living leaves; but in Stigmatea there is a very minute ostiolum, and in Parodiella none at all; hence the latter suggests Perisporiaceae.

In the subfamily Melogrammeae the perithecia are either formed from the stroma or confluent with it, and are not carbonaceous, but tough and coriaceous, sometimes soft, but not brittle, and occasionally coloured. They are densely caespitose, but usually almost free at the apex, and destitute of any definite neck. In most cases the tufts, or clusters, are erumpent, connate below, and confluent with the stroma. In habit approaching to Diatrypeae rather than to Dothideoideae, but the perithecia are more distinct and clustered, as in Cucurbitaria, and not confluent above, so as to form a disc. The genus Sarcoxylon is rather a remarkable one, as it forms a globose stroma, in one species as large as an orange, and solid, with the perithecia sunk in the substance, and over the whole surface, as in Daldinia; but the crust is soft and never carbonaceous, and the perithecia are thin and membranaceous. The sporidia are coloured, and hence it is analogous with some species of Xylaria. Botryosphaeria is a rather numerous genus, with erumpent, botryoid, or grape-like clusters of perithecia, analogous to Cucurbitaria, but less distinct; in the majority of species the sporidia are large and hyaline, consisting of a single Endothia resembles Diatrype in habit, with a bright cell. yellow stroma. Fuckelia contains species which resemble an erumpent Hypoxylon, having a subglobose stroma with immersed perithecia; but the substance is tough and rather flexible, not at all carbonaceous or brittle. The sporidia are

brown and without septa. Camarops in habit is just an effused Hypoxylon, but the stroma is soft, and the sporidia septate and brownish. The genus Melogramma, as limited by Saccardo, has sporidia which are continuous and brown. The stroma is erumpent, and then almost superficial, and the numerous perithecia are aggregated in a similar manner to Botryosphaeria, although sometimes effused. As expanded by ourselves, this genus includes as subgenera species which correspond to the type in habit and general appearance, but vary in the form and septation of the sporidia. It may be intimated here that the genus Valsaria, as characterised by Saccardo, which has coloured and uniseptate sporidia, includes three different types of stroma-that of Melogramma, that of Diatrype, and that of Valsa, or rather of Pseudovalsa. In our arrangement we refer each of these groups, as subgenera, to the species indicated above. Thus the Melogrammoid Valsariae will be found under the subgenus Valsariae of Melogramma.

The subfamily Diatrypeae differs at sight from Melogrammeae in the perithecia being immersed in a stroma of a different character, and consequently not superficially visible, and in the substance being carbonaceous. In some cases the species are broadly effused and crustaceous, and then resembling effused species of Hypoxylon. In some other cases the stroma is flattened and discoid, the imbedded perithecia being indicated by the punctate ostiola; whilst in a few other cases the erumpent stroma is wart-like, and the convex surface marked with prominent ostiola. The typical genus *Diatrype* has an erumpent stroma, which is effused, or discoid, or wart-like. Those of the latter kind, or with a wart-like stroma, but which have asci containing a great number of sausage-shaped hyaline sporidia, are included in the subgenus Diatrypella. The species which have similar sporidia, but only eight of them in each ascus, whether the stroma be verrucaeform or discoid or effused, constitute the typical Diatrype. Other species, with the external characters of Diatrype, but with other than sausage-shaped and hyaline sporidia, will be found under the several subgenera of the one genus Diatrype, which represents the sub-family Diatrypeae. Practically there would be no difficulty for a student in the way of discriminating species of Diatrypeae from any other subfamily except the *Valseae*, next to be enumerated, whilst a little experience will soon enable him to surmount this temporary difficulty.

The subfamily Valseae contains an immense number of species, which are pustular and erumpent. The stroma is formed from the altered matrix. The perithecia are quite distinct, and mostly arranged in a circle, with convergent necks. The principal genus is Valsa, in which the perithecia are collected in more or less definite clusters, immersed in the bark of trees or of their branches and twigs, and either disposed in a simple circle or a circular group, with the necks converging towards the centre, so as to form an erumpent disc, which splits the bark (Fig. 99). The sporidia are hyaline, and either continuous or septate according to the subgenera. The largest

number of species have small hyaline sausage-shaped sporidia, which is the typical Valsa. Those in which the sporidia are more than eight in each ascus are either Valsella or Coronophora, as subgenera. When the sporidia are only eight, the species are again subdivided into those in which the ostiolum is sulcate,



FIG. 99.—Perithecia of Valsa.

as Eutypella; and into those in which the ostiolum is not sulcate, but the disc is whitish, gray, or yellowish, and then called Leucostoma; or the ostiolum is not sulcate, and there is no pallid disc, which is Euvalsa, or true Valsa. In two other small subgenera, with like sporidia, when the perithecia are four in a group, or a small number, it is Quaternaria; and when a larger number, and loosely disposed, or free, then Calosphaeria; and thus the series of the species of Valsa with sausage-shaped sporidia is complete. In a second section with simple hyaline sporidia, these are of some other form than sausage-shaped, as represented by the subgenera Cryptosporella and Cryptospora. In a third section the sporidia are still colourless, but septate, that is to say, uniseptate in Chorostate and triseptate in Calospora. Closely resembling Valsa in habit, or external appearance, is the genus Melanconis (Fig. 100), in which the sporidia are uniseptate, and either hyaline or coloured, accompanied by or associated with a conidial stage, which resembles the stylosporous genus

Melanconium. In some of the species the ascigerous perithecia have been found growing in the midst of the pustules of conidia, and in others closely associated in contiguous pustules.



FIG. 100.—Stroma and perithecia of *Melanconis*.

In another genus, that of *Pseudovalsa*, the sporidia are septate and coloured, but there is no *Melanconium* to which the species are related. When the sporidia are uniseptate they fall into the subgenus *Valsaria*, but when three or more septate into the subgenus *Aglaospora*. Only one other genus of the *Valseae* remains to be alluded to, and that is *Fenestella*, in which the sporidia are multiseptate, and divided in both directions so as to be muriform

It may be intimated that of the species of or clathrate. genuine Valsa, with sausage-shaped sporidia, very many of the species are genetically connected with species of Cytospora, a genus of Sphaeropsideae, in which the spores are also sausage-shaped and hyaline, but without asci, being produced on short slender threads within a kind of spurious compound receptacle which greatly resembles Valsa in appearance. These conidia are often found growing on the same twigs as Valsa, or upon twigs upon which the Valsa appears subsequently, but the precise influence of the one upon the other has not yet been demonstrated. Other species of the Valseae have been named in conjunction with species of other genera of Sphaeropsideae, but less universally. In like manner species of Pseudovalsa are related to the similar, but stylosporous, fructification of species of Coryneum.

The last subfamily is *Eutypeae*, and here the leading feature, as distinct from *Valseae*, is that the stroma is broadly and indefinitely effused, being formed from the more or less changed matrix. The perithecia are immersed in the stroma, and for the most part are densely and broadly gregarious. *Eutypa* is the typical genus, often occurring on naked wood, the substance of which is transformed into a stroma, in which the perithecia are immersed. In about half the species the ostiola are sulcate, and in the other half they are not. The

asci contain eight sausage-shaped hyaline sporidia. A closely allied genus is *Cryptovalsa*, which conforms externally to *Eutypa*, but the asci contain respectively more than eight similar sporidia.

The other genus contained in this family has the stroma commonly less broadly effused, and the species are more rare on wood than on the bark of branches, twigs, and the stems of herbaceous plants. The ostiola are often very much elongated, and the surface of the stroma is usually blackened. The great feature in which this genus differs from the preceding is in the fruit: although the asci are octosporous, the sporidia are typically fusoid and colourless, replete at first with four guttules or minute oil-drops, and at length often uniseptate, or in some cases triseptate.

The compound Sphaeriaceae for the most part may be recognised at once by the naked eye, on account of their larger size, from the agglomeration of perithecia, and the presence of a stroma, or bed, on which they are placed or immersed, and which of itself partakes of a definite form. In all systems of elassification prior to Saccardo, the compound and simple Sphaeriaceae were kept apart, and were recognised as separate groups, which certainly facilitated identification by the student. Under the system promulgated by Saccardo, there is no distinction of that kind, but all are mixed together and classified according to their sporidia. Convinced that this was practically an error, we undertook a rearrangement of the Pyrenomycetes, in which the compound and simple were kept distinct, whilst most of the new genera were accepted. This scheme was embodied in Synopsis Pyrenomycetum, published in 1884 to 1886.

The section of the Sphaeriaceae which includes the Simplices, or genera in which the perithecia are distinct from each other, and not combined in or upon a common stroma, is even more numerous in species, and may be described in like manner under the several subfamilies. The connecting link is the subfamily *Cucurbitarieae*, in which the perithecia are densely gregarious or caespitose, and for the most part form large erumpent clusters. In *Nitschkia* the black perithecia are mostly clustered upon a thin whitish mycelium, the asci

are octosporous, and the sporidia are small, hyaline, and cylindrical. In *Fracchiaea* the perithecia are aggregated upon a sort of stroma like a crust; the asci, except in one species, contain numerous simple hyaline sporidia. *Gibbera* and *Gibberidea* have caespitose perithecia, which in the former are persistently setulose, and in the latter soon become smooth; in both cases the sporidia are septate and hyaline or brown. In the two remaining genera the habit is more typical, the pustules being erumpent; and in *Otthia* the sporidia are uniseptate, whilst in *Cucurbitaria* the sporidia are typically muriformly septate and coloured, whilst in small subgenera they are either continuous or septate and brown.

The ninth subfamily includes the *Superficiales* of Fries, in which the perithecia are quite distinct, and superficial or nearly so, aggregated together or scattered. These may be further subdivided into the *Byssisedae*, *Villosae*, *Roselliniae*, and *Sordariae*. In the *Byssisedae* the perithecia are seated upon a byssoid or felted stratum called a subiculum (Fig. 101). The genus *Byssosphaeria* contains species in which the perithecium is



FIG. 101.—Byssosphaeria, with section of perithecium, ascus, and sporidia.

smooth or naked, with the sporidia varying according to the several subgenera, from simple or continuous to multiseptate or muriform, and hyaline or coloured. In *Chaetospheria* the perithecia are villose, and also seated upon a subiculum. In *Villosae* there is no subiculum, but the perithecia are woolly, downy, or setulose. The principal genus is *Lasiosphaeria*, in which the sporidia are hyaline, or but

slightly coloured. In *Coniochaeta* the sporidia are distinctly coloured. In *Venturia* the perithecia are membranaceous and setulose, growing for the most part on leaves, and the sporidia are oblong and hyaline, continuous or septate. *Chaetomium* is a genus easily recognised, by its fragile bristly perithecia, diffluent asci, and continuous brown sporidia, which are often almond-shaped. *Rosellineae* almost corresponds to the *Denudatae* of Fries, with the perithecia almost or quite superficial, smooth and naked, and mostly

The numerous genera which are recognised carbonaceous. by Saccardo, having hyaline sporidia, have been reunited under the genus Psilosphaeria, the different forms of sporidia being recognised by subgenera. Another genus, Rosellinia, includes the species with coloured sporidia without septa; and Melanomma those species with coloured septate sporidia, in conjunction with the smaller genus Ohleria. Sporidia which are divided in both directions, so as to be muriform, In appearance the subfall under the genus Strickeria. division of Sordarieae is almost equal to Rosellineae; but, instead of being carbonaceous, the perithecia are membranaceous, and nearly all the species flourish on dung. In many instances the sporidia are involved in a gelatinous coat. There are really but two distinct genera, although, on account of modifications in the sporidia, several subgenera are accepted, which some authors have raised to the rank of genera. Sordaria is, as a whole, a very characteristic genus, which the late Dr. Winter made the subject of a monograph. The sporidia in the majority of species are large, elliptical, and brown, sometimes with a hyaline tail, but in one subgenus they are uniseptate. The other genus, Sporormia, has a peculiar form of fruit which calls to mind Perisporium ; most of the species are very minute, almost invisible without a strong lens, and the sporidia are brown and septate, readily breaking up at the joints.

In the old arrangement of the Simple Sphaeriaceae adopted by Fries, the *Superficiales* were succeeded by a group of genera in which the perithecia were smooth and half immersed in the matrix. The base of the perithecium being flattened, they possessed a more or less conical form, and were occasionally only adnate, although apparently half immersed. These were the *Pertusae*, which we constitute the tenth subfamily; and the typical genera are *Conisphaeria*, in which the sporidia are hyaline; and *Amphisphaeria*, in which the sporidia are coloured. Another genus, under the name of *Ticothecium*, includes minute species, found growing upon Lichens. Such species as conform in general habit and appearance, but with muriform sporidia, find a place in the genus *Teichospora*. This last subfamily leads almost imperceptibly to the two

following, in which the perithecia are more and more immersed, until they entirely disappear in the matrix. These are the *Lophiostomaceae* and the *Endoxyleae*, the *Ceratostomeae* being rather a parallel than a consecutive series.

The Lophiostomaceae find a place in the Sylloge as a separate group, and are regarded as a link between Hysteriaceae and Sphaeriaceae, on account of the broad compressed mouth of the perithecia; there is, however, no real affinity, but rather analogy, between them. This subfamily includes the Sphaeria platystomae of Persoon, and consists of species which are simple in habit, with the base of the perithecium flattened and adnate, or partially imbedded in the matrix, so as to be subsuperficial. In texture they are mostly hard and carbonaceous, with the broad ostiolum more or less compressed, opening by a very narrow fissure. The sporidia are very variable, except that the hyaline continuous form is absent. There is but one genus in all the seven sections based upon the character of the sporidia, according to Saccardo's arrangement, but which we unite in three genera-Lophiosphaera, with hyaline sporidia; Lophiostoma, with coloured sporidia; and Lophidium, with muriform sporidia.

Parallel with this and the succeeding subfamily must be placed the Ceratostomaceae, in which the perithecia are usually immersed, but sometimes subsuperficial, either somewhat carbonaceous or almost membranaceous-two genera to the former. and one to the latter. In Ceratostomella the sporidia are hyaline, and in Ceratostoma coloured. In their entirety they were formally included by Fries in his Sphaeria Ceratostomae, on account of the elongated beak-like ostiolum. The remaining genus Gnomonia, with submembranaceous perithecia, contains minute species, usually growing on dead leaves or petioles, with the long ostiola protruding like bristles. The habit is the same in the subgenera, but the sporidia are continuous, uniseptate, or rarely triseptate, or still more rarely thread-like, but always uncoloured.

In sequence from the *Lophiostomaceae* follows the thirteenth subfamily, *Endoxyleae*, which corresponds to the *Sphaeriae immersae* of Fries. The perithecia are immersed in the matrix, usually rotten wood, with only the short erumpent

necks of the perithecia visible on the surface. The small genus *Endoxyla* includes such species as have sausage-shaped sporidia, which are slightly coloured. The bulk of the species are included in *Xylosphaeria*, having sporidia somewhat elliptical, either continuous or septate, and brown. Here again the subgenera include the various types of sporidia, for in *Anthostoma* they are continuous, in *Phaeosperma* uniseptate, in *Kalmusia* three, or more, septate; and those with muriform sporidia are relegated to be a distinct genus under the name of *Thyridium*, on account of a sort of effused woody stroma in which the perithecia are immersed.

From these lignicolous or wood-inhabiting groups we pass to the subfamily Obtectae, which almost corresponds to the Sphaeriae obtectae of Fries. The perithecia are innate, growing on bark, and covered by the cuticle. One of the most notable genera is Massaria, in which the sporidia exude from the perithecia, and blacken the matrix around the ostiola. The sporidia are nearly always involved in a hyaline gluten, and many of them are very large and beautiful. In the typical section they are two, or more, septate, and coloured; but in the subgenus Massariella only uniseptate, and in the subgenus Massarina multiseptate, but uncoloured. The subgenus Pleomassaria includes such species as have muriform sporidia. In fructification this genus corresponds to Pseudovalsa amongst the composite Pyrenomyceteae, but differs, of course, in the distinctly scattered perithecia and the mucous envelope of the sporidia. In the genus Cryptosphaeria we encounter a remote resemblance to the Eutypeae; for the perithecia are densely gregarious, sometimes in patches of some inches in length, but without stroma of any kind. The perithecia are smooth and naked, and the sporidia sausageshaped and hyaline. In Enchnoa the perithecia are fewer and scattered, but externally pilose. Another genus which includes only species with hyaline continuous sporidia is Physalospora, in which the perithecia are scattered over twigs and branches, covered by the cuticle, so as only to be recognised by the slight elevations with the central dot of the ostiolum. In Endophlaea the habit is similar but the sporidia different, being one or more times septate; as, for instance, in

the subgenus Didymella uniseptate, and in Metasphaeria. The small genus Ophiobolus corresponds to the multiseptate. genus Raphidospora in the Caulicolae, in which the sporidia are filiform. Of genera with coloured sporidia Anthostoma includes those which are continuous; and Didymosphaeria. those in which the sporidia are uniseptate. Leptosphaeria has the sporidia multiseptate, but the coloration is often very Other species of Leptosphaeria which grow slight. on herbaceous plants will be found under Heptameria in the Caulicolae; in fact, the separation of the two families Obtectae and Caulicolae is a purely arbitrary one. Delacourea, again, includes such species of *Pleospora* as are found growing on the twigs of trees and shrubs, having coloured muriform sporidia.

The fifteenth subfamily, Caulicolae, includes such species as conform in habit to Obtectae but are found on the dead stems of herbaceous plants. In the genus Phomatospora the sporidia are continuous and hyaline, hence corresponding to Physalospora. In Apiospora the rather unusual form of sporidia is found in which, though practically uniseptate, the lower cell is small, consequent on the septum being placed near the base. In Didymella the sporidia are uniseptate and hyaline, and correspond to the subgenus Didymella of Endophlaea. Metasphaeria is a large and important genus of Caulicolae, in which the sporidia are multiseptate and hyaline. Raphidospora includes such caulicolous species as possess very long thread-like sporidia, which may or may not be divided by transverse septa into short joints. Of species which have coloured sporidia those in which the sporidia are continuous will be found in the genus Anthostomella, those with the sporidia uniseptate in Didymosphaerella, and with the sporidia multiseptate in Heptameria, corresponding to Leptosphaeria. This is one of the largest genera on herbaceous plants. Pleospora is a well-known genus in which the perithecia are often large, and become erumpent. The sporidia are muriform and coloured. Some species or other may be anticipated on the dead stem of almost any herbaceous plant. The genus Pyrenophora differs from *Pleospora* in the perithecia being selulose, but the sporidia the same (Fig. 102).

The sixteenth subfamily is the Foliicolae, which, as the

name suggests, are normally found growing on leaves, sometimes living and sometimes dead. The former are more or less destructive parasites, and are found not only on the leaves

of trees and shrubs, but also on herbaceous plants, and on the fronds of Cryptogams. The perithecia are immersed in the substance of the leaf, sometimes scattered, but often in groups. They are thin and membranaceous, usually minute, and perforate at the apex. When growing upon living leaves they are mostly seated on discoloured spots, caused probably by the delicate mycelium destroying the vitality of the cells. Similar blanched spots, with analogous minute perithecia seated upon them, are to be met with in several genera of Sphaeropsideae, such as Phyllosticta, Septoria,



FIG. 102.—Asci and sporidia of Pleospora.

etc.; but the asci are absent, and the minute sporules are produced at the tips of slender sporophores. In certain cases these are believed to be in some manner connected with foliicolous *Sphaeriae*, as a stylosporous or imperfect condition, but how they are connected has not yet been determined. Of the genera in this subfamily *Laestadia* has the sporidia continuous, or without septa; in *Sphaerella* they are uniseptate, and are very numerous in species. In *Sphaerulina* the sporidia are either three or many septate. Under this genus are included the foliicolous species of the genera *Metasphaeria* and *Leptosphaeria*, so that in some the sporidia are slightly coloured. In one other genus, that of *Linospora*, the sporidia are very long and thread-like.

The last subfamily is that of *Microthyriaceae*, and this is somewhat of an outside group, as the perithecia are different in form and structure, being superficial, or nearly so, either membranaceous or somewhat carbonaceous, dimidiate and flattened almost like a shield, formed of radiating cells, and either pierced with a pore in the centre or without one. The genus *Microthyrium* seems

to be almost analogous to that of *Asterina* in the *Perisporiaceae*. In this genus the perithecium is flat and membranaceous. Amongst the subgenera, *Myiocopron* has continuous sporidia; in the typical subgenus they are uniseptate, and in *Seynesia* the uniseptate sporidia are brown. In the genus *Clypeolum* the perithecia are carbonaceous, and shield-like, with uniseptate hyaline sporidia; or in the subgenus *Vizella* continuous and brown. In the subgenus *Scutellum* they are septate and coloured. The two remaining genera are *Micropeltis* and *Pemphidium*; in the former the perithecia are convex and the sporidia multiseptate and hyaline; in the latter the perithecia are scutate, the nucleus gelatinous, and the fusiform sporidia brown.

Polymorphism of a somewhat elaborate form has been credited to some of the Pyrenomyceteae. Take, for instance, the very common Pleospora herbarum, on dead stems. That ubiquitous black mould, Cladosporium herbarum, has been recorded as one conidial form. This also has been suspected of merging into Macrosporium commune, which again has been named as a form of conidia of the same Pleospora. By a further development the Macrosporium, in some occult manner, appears with the spores in chains, and then again, under the name of Alternaria tenuis, is referred to the Pleospora; so that three supposed species of Dematicae have been recorded as conidia of Pleospora herbarum. Then again one of the Sphaeropsideae, having perithecia, but with stylosporous fruit and named Phoma herbarum, has been called the spermogonia of the same Pleospora. At the same time it may be asked what function is ascribed to these spermogonia; for if, as M. Cornu has suggested, they are capable of germination, then the small sporules are not spermatia, or fecundating bodies, as the name would imply, but have some other function. What again are the bodies termed pycnidia? Until the process has been traced, for at present it is little more than suspected, accurate phraseology cannot be applied. Conidia, of various forms, and for the most part of the nature of Hyphomyceteae, are common enough, and possibly produce a mycelium upon which perithecia are afterwards developed, but so much is at present only a matter of faith, which remains for the future to demonstrate.

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CHAPTER XVIII

GAPING FUNGI-HYSTERIACEAE

THE Hysteriaceae are related on the one hand to the Pyrenomycetaceae, and on the other to the Discomyceteae, but perhaps externally most strongly to the former, to which they approach through the subfamily Lophiostomaceae, whilst their connection with Discomyceteae must be through such genera as Colpoma As the *Discomyceteae* approach Lichens and Triblydium. through some of the Patellariaceae, so also do the Hysteriaceae through Aulographum and Dichaena. In this family the perithecia are erumpent and then superficial, with a flattened base, and horizontally extended, either oblong or linear. In substance they are occasionally membranaceous, but more often coriaceous, or rather carbonaceous, but very rarely somewhat fleshy. They are for the most part black, and dehiscence takes place by a long narrow fissure which extends the whole length of the perithecium. The asci may be tetrasporous or oetosporous, and sometimes polysporous, but the sporidia vary in the different sections and genera, from simple and continuous to multiseptate and muriform. The arrangement proposed by Saccardo may be accepted as the best yet proposed. The only objection which could be urged concerns the genera Schizothyrium, Aulographum, and Lembosia, which from our point of view seem to be scarcely generically distinct, since the difference lies only in the sporidia, which are respectively continuous, uniseptate, and hyaline, and uniseptate and coloured. Great care needs to be exercised, for species of Aulographum are at first continuous, as in Schizothyrium, and may ultimately be faintly coloured, passing thus into Lembosia.

The whole family is divided, carpologically, into nine sections,

GAPING FUNGI-HYSTERIACEAE

Hyalosporae, in which which may be referred to in their order. the sporidia are continuous and hyaline, includes the two genera Schizothyrium and Henriquesia. In the former the sporidia are minute, and in the latter large; but the habit is also different, the species being small and superficial, mostly occurring on leaves and herbaceous stems in the former; and erumpent, Hysterium-like, and arboricolous in the latter. The analogue of Schizothyrium, in the Sphaeropsideae, is Labrella, which resembles Schizothyrium in habit and appearance, but the perithecia are stylosporous, and in some species may prove to be genetically related. The Phaeosporae differ from Hyalosporae in the continuous sporidia being distinctly coloured. The only genus is Farlowia, in which the habit is distinctly that of Hysterium, to which the species were formerly referred, and the perithecia carbonaceous. The British representatives are the Hysterium Carmichaelianum of Berkeley and the Hysterium repandum of Bloxam, which hitherto are the only species known. The Hyalodidymae are characterised by hyaline uniseptate sporidia, and include four genera, in one of which, Aulographum, the perithecia are membranaceous, already alluded to; in Glonium and Actidium the perithecia are carbonaceous, in the former being simple or branched, and in the latter stellate. There is considerable difference in the habit of the different species of Glonium, some being linear and scattered, whilst others are densely agglomerated in compact heaps. There is still a fourth genus, that of Angelinia, in which the perithecia are at first somewhat fleshy, and open, exposing the disc, so that it resembles Cenangium. The colour of the excipulum being reddish, is also abnormal, and the single species is rather a doubtful member of the Hysteriaceae. The Phaeodidymae, with coloured uniseptate sporidia, includes the two genera Tryblidium and Lembosia. In the former the perithecia are gaping, with swollen lips, exposing the hymenium more than usual in this subfamily. Its nearest ally is Tryblidiella, in the Pheophragmiae section, and the two supposed genera differ only in the latter having sporidia with more than one septum, whilst in the former they are only uniseptate, for which reason we are disposed to regard the distinctions as only of subgeneric value. Lembosia has also been referred to already

as representing Aulographium, with coloured sporidia. The Phaeophragmiae is the largest section in this subfamily, having six genera and a large number of species. The genera are arranged in two groups, in one of which the lips of the perithecia are obtuse and rather distant, and in the other acute and connivent. In the former is placed *Tryblidiella*, already mentioned as a triseptate condition of Tryblidium and Hysterium, the typical genus, in which the lips are so connivent that the disc is rarely exposed, except when moist. The perithecia are carbonaceous and even, with three-septate or multiseptate coloured sporidia. Corresponding species, with sporidia uncoloured, have been transferred to the genus Gloniella, and species with muriform sporidia to Gloniopsis and Hysterographium. The third genus of Phaeophragmiae is Rhytidhysterium, in which the perithecia are striate or sulcate, and resemble a Lichen without a thallus. Hitherto the genus is confined to South America. In one other genus of the first division the asci are polysporous, and Baggea has but one species, which has been found in Northern Europe. The two remaining genera, which constitute the division with thin connivent lips, are *Mytilinidion* and *Ostreion*. In the former the asci are octosporous and in the latter tetrasporous. Mytilinidion has the perithecium, in typical species, vertical and compressed, after the manner of Lophium, with the lips very acute, and firmly The other genus, Ostreion, originally denominated closed. Ostreichnion, but, as we think, unwisely changed for insufficient reasons by Saccardo into Ostreion, has perithecia which in form resemble an ovster, placed vertically, and resting on the hinge. The sporidia are four in each ascus, which, in the only recognised species, are very large and multiseptate. The sixth section is Hyalophragmiae, in which the multiseptate sporidia As already intimated, Gloniella is analogous to are hyaline. Hysterium, with hyaline sporidia, and consequently the perithecia are carbonaceous; but in Pseudographis the perithecia are coriaceous, and gaping, with precisely the habit of Try-Arranged according to natural blidium and Tryblidiella. affinities, these three genera would be consolidated, and the three forms of fruit recognised only as subgeneric distinctions. The genus Dichaena approaches Lichens in its habit of growing

GAPING FUNGI-HYSTERIACEAE

on living bark, aggregated in dense patches, and the perithecia are elliptical and irregular. A condition may often be met with in which no asci are developed, but these are replaced by stylospores. This condition has been referred to Sphaeropsideae, under the generic name of Psilospora, whilst other authors simply mention it as the pycnidia of Dichaena. There is little doubt of its being an imperfect condition of this Hysteriaceous The section Hyalodictyae includes the one genus genus. Gloniopsis, in which the sporidia are muriform but hyaline. The habit and texture is that of Hysterium. In the same manner, species of the old genus Hysterium which have muriform coloured sporidia find a place in the section Phaeodictyae under the genus Hysterographium. The ninth section is Scolecosporae, in which the sporidia are very much elongated, so as to be thread-like, or rod-like, and hyaline. The one genus in which the sporidia are cylindrical, and much shorter than the asci, is Hypoderma. The perithecia are membranaceous, and flattened, with a narrow fissure, and the species are most commonly found on dead leaves, herbaceous stems, and occasionally on young twigs. Sometimes several perithecia grow on irregular bleached spots, and these are often accompanied by smaller perithecia, which contain only minute stylospores, belonging technically to the Sphaeropsideous genus Leptostroma, but which are often called the spermogonia of the various species of Hypoderma. It must not be assumed that the term spermatia, applied to the minute bodies enclosed in the smaller perithecia, indicates fecundative functions, since no sexuality has been proved. In the remaining genera the sporidia are truly filiform. Lophodermium has the habit and appearance of Hypoderma, but the sporidia are different, and in like manner the species are often associated with forms of Leptostroma. Lophium is a small genus with rather carbonaceous perithecia of a shellshape, as mentioned under Mytilinidion, with very acute connivent lips. Sporomega has depressed, and rather coriaceous, perithecia, with thick gaping lips, which partially expose the disc (Fig. 103); and Colpoma resembles it in these features, but differs in being developed beneath the cuticle, which is for a long time adpressed, or adherent to the lips, and the substance is softer. In habit it resembles Tryblidium rather than

Sporomega. The last genuine species is Ostropa, in which the perithecia are almost sphaeroid, dehiscing above with a longitudinal fissure, thus suggesting relationship with the



FIG. 103.—Sporomega with enlarged perithecium and ascus. Lophiostomaceae. The rather aberrant genus Robergea is sometimes placed here, as having affinity with Ostropa; but Acrospermum appears to us to be more closely related to Hypocreaceae, from the absence of any apical fissure.

The total number of species in this subfamily may be accepted as 450, and of these some have a very wide geographical distribution. It is an open question whether the family is most closely allied to the *Pyrenomyceteae* or the *Discomyceteae*. The consolidation of the hymenium into

a disc, and the strong development of the paraphyses, indicate relationship with *Discomycetes*, and this is supported by the almost universal subsuperficial habit. This is not, however, a question of practical importance, and may be compromised by placing the *Hysteriaceae* as an intermediate group between the *Pyrenomycetes* and the *Discomycetes*.

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CHAPTER XIX

CONJUGATING FUNGI-PHYCOMYCETES

THE comparatively small order of fungi known as the *Phycomycetes* has been subjected to more exact examination and clearer definition than when Berkeley called it *Physomycetes* in 1857, and limited it by the definition of "fertile cells, bladder-shaped, scattered on the threads which are not compacted so as to form a distinct hymenium. Sporidia indefinite, formed from the protoplasm of the cells." It will be observed that this diagnosis only takes cognisance of the superficial, and asexual, reproduction by gonidia, produced within sporangia, the latter being scattered over the threads, as in typical forms of *Mucor*.

Technically, as at present recognised, the *Phycomycetes* are characterised by a unicellular mycelium, often parasitic on plants or animals, sometimes saprophytic, developed in the air or in water. Reproduction sexual or asexual. Sexual by oogonia and antheridia, or by conjugation, producing zygospores. Asexual by means of gonidia or zoospores. Many of them resemble, more or less, the moulds in external appearance, having conspicuous hyphae, arising from a procumbent creeping mycelium—but that the latter threads are without septa, and the former may either produce sporangia or naked gonidia. Moreover, they are further removed from the moulds by possessing, in addition to the conspicuous agamic reproduction, a true sexual method by means of oogonia fertilised by antheridia, or by zygospores resulting from conjugation of specialised branches.

Undoubtedly there is considerable variability in the external features of the different families constituting this

order, which includes the old typical Mucors and their allies-almost the sum total of the Physomycetes of former times; and also the *Peronosporeae*, or rotting moulds, previously classed with the Hyphomycetes; as well as the "white rusts" (Cystopi), formerly united with Uredines. In addition to these are the fish moulds, or Saprolegniaceae; and the insect moulds, or Entomophthoraceae; so that altogether there are four very distinct families, with well-developed hyphae; to which must be added two other, inferior, groups, in which the hyphae are obsolete, for a long time regarded as outside families, with obscure affinities, but remotely associated with the Uredines under the names of Chytridium, Synchytrium, and Protomyces. This association of apparently rather heterogeneous elements is held together by the conservating bond of a dimorphic reproduction; otherwise their relationship is, at first sight, so obscure that it will be necessary to advert to each family separately.

It has already been intimated that four of the families possess a conspicuous vegetative system, in a unicellular creeping mycelium, giving rise to erect, simple, or branched threads, which bear the conidia, or otherwise asexual repro-Although agreeing in this, the organs themductive organs. selves differ considerably in the four families, inasmuch as the Mucoraceae develop cysts, or bladder-like cells (sporangia), which enclose either many or only one reproductive cell, or These cysts are terminal on the fertile hyphae, gonidium. and may be produced singly or in clusters. In the Peronosporaceae there are no true cysts, but naked gonidia, which may be passive, and germinate directly, or their contents may become differentiated into zoospores, or zoogonidia; that is to say, active ciliated zoospores, which at length become passive and germinate. The Saprolegniaceae are aquatic, and produce zoospores within the changed hyphae; and the Entomophthoraceae are parasitic on insects, and develop single conidia on short sporophores. Thus it will be seen that there are distinct features in the asexual reproduction of the four families sufficient for their discrimination. It may be added, as a further distinction, that the Mucoraceae are saprophytic on dead animal or vegetable substances. The Peronosporaceae

CONJUGATING FUNGI-PHYCOMYCETES

are parasitic on living vegetables. The Saprolegniaceae are aquatic. And the Entomophthoreae are entomogenous.

The *Mucoraceae* might be mistaken for moulds if not more closely examined. The erect threads are not conidia-bearers,

but sporangiophores, because they support sporangia at their tips; and these sporangia are nearly globose cells of thin membrane, which enclose the spores, or reproductive bodies (Fig. 104). When fully matured the sporangium is ruptured and the enclosed spores escape. This is the ordinary asexual reproduction of the Mucors, and all that was really known of them half a century ago. In some cases the fertile branch, or sporangiophore, is



FIG. 104.-Mucor.

prolonged into the interior of the sporangium, and becomes a columella.

The sexual reproduction of the *Mucoraceae* is accomplished by zygospores, resulting from conjugation, and hence they are sometimes characterised as *Zygomycetes*. In many of the species this form of reproduction has never been traced, but has been accepted from analogy. Two lateral branches resembling each other, and termed *archicarps*, are concerned in the process. They resemble at first ordinary branches, which approach each other until the tips meet, but as they increase in size they



FIG. 105 .- Formation of Zygospore. After De Bary.

crease in size they become clavate, and are densely filled with protoplasm. At length the extreme portion of each archicarp is separated from the basal portion by a transverse septum, each portion acquiring a distinctive name, the basal cell being termed the

suspensor, and the apical cell the gamete (Fig. 105). At the point where the two gametes meet the separating cell-walls are

soon dissolved, so that the contents coalesce, and a single cell is constituted from the union of the two gametes, which is, in effect, the young zygospore. Henceforward the cell-wall of the zygospore becomes thickened, and coloured, so that it usually acquires a brown colour, and is warted or spinulose when mature. The zygospores thus formed are also characterised as *resting spores*, because they are capable of resting, or remaining in a dormant condition for months before germination takes place, usually through the winter, becoming active in the spring.

It may sometimes happen that the two gametes, instead of coalescing, remain distinct; or in rare cases only one archicarp is produced; yet in such instances a body resembling a zygospore is developed, without conjugation, and therefore the resultant spore is called an *azygospore*. In some species the zygospores are produced freely, and in considerable number, amongst the ordinary vegetative hyphae, at the same time, or succeeding, the production of the ordinary gonidia; but the latter germinate at once, without any period of rest, and hence they do not survive through the winter. Usually the development of gonidia is arrested in the autumn and the formation of zygospores commences. In the absence of zygospores the mycelium becomes perennial, and thus survives the winter, so that the species may be perpetuated. Provision is thus made for reproduction, asexually, by means of gonidia, which germinate at once; by azygospores, which germinate after a period of rest, and sometimes by a perennial mycelium, which survives the winter; and sexually by the production of zygospores, which accrue from the conjugation of two approximating specialised branches of the hyphae.

The *Peronosporaceae* are, in their typical forms, more nearly resembling the *Mucedines* in habit than are the *Mucoraceae*. The erect hyphae, or gonidiophores, are usually furcately branched two or three times, and bear the gonidia (Fig. 106), as more or less elliptical hyaline bodies, at the ends of the branches. These constitute the means of asexual reproduction, and may be developed successively or simultaneously. In some cases the gonidia so produced appear to be simple gonidia, but in others they undergo transformation; in the former case they

CONJUGATING FUNGI-PHYCOMYCETES

germinate at once through a lateral pore, but in the latter case an intermediate stage intervenes. Each gonidium when mature has more turbid contents, which are seen to accumulate in several centres, and then to become divided by the growth of a membrane about each segment, into distinct inner cells,

each with a nucleus. Soon the wall of the mother cell is ruptured, and the contents escape, now differentiated into three or four, or more, smaller but similarly shaped bodies, armed with a pair of vibratile cilia, by means of which they move actively in any drop moisture with of which they may come in contact, trans-



FIG. 106. -Gonidiophore of Peronospora.

formed into secondary gonidia or *zoogonidia*, sometimes called zoospores. In this condition they move about for some time over the moist surface of the leaf upon which they are discharged, until at length they come to rest, lose their cilia, and commence germination, by the production of a delicate germ-tube which enters the stomata of the fostering plant, and form a mycelium beneath the surface. From this mycelium spring erect hyphae, which seek the air, and, becoming branched, constitute new gonidiophores, and the cycle is complete.

The sexual reproduction takes place within the host-plant, by the production of oogonia upon branches of the mycelium. They originate as spherical swellings at the end, or intercalated in the hyphae, and after a time reach a considerable volume, and contain a dense protoplasm with oil drops. Soon these swellings are isolated by the production of a septum across the hypha when terminal, or above and below when intercalary. After this differentiation of the oosphere takes

place, by the concentration of the denser portion in the centre, in the form of a sphere, involved in a delicate membrane, surrounded by a hyaline layer of protoplasm. At this time the *antheridium* is being developed from a lateral branch of the hypha, just below the oogonium (Fig. 107). When fully developed this organ is elliptical or obovate, smaller than the oogonium, and filled with granular protoplasm; cut off at the base from connection with the hypha by a transverse septum. Assuming that the oosphere is formed, and the antheridium perfected, the latter comes in contact with the former, and, at the point of contact a slender tube is projected through the wall of the oogonium, which grows until it reaches the surface of the



FIG. 107.—*Peronospora.* a, young state; b, formation of oosphere; c, after fertilisation. After De Bary.

Meanwhile the contents of the antheridium underoosphere. go change : towards the centre they are more dense, and, as the fertilisation tube becomes complete, this portion passes down it and mingles with the protoplasm of the oosphere, and the connection is complete. The oosphere is fertilised, and, secreting a thick wall, becomes an oospore, a resting spore, analogous to the zygospore of the Mucoraceae. Gradually, by the decay and dissolution of the hyphae, these oospores become free, hybernating amidst the decaying tissue of the foster-plant, and awaiting rejuvenescence in the spring. When the latter period arrives the contents of the oospore, in most species, become differentiated into a host of minute active zoospores, similar to those evolved from the differentiated gonidia, and, by rupture of the wall of the mother cell, become diffused and ready to attach and establish themselves upon young seedlings

CONJUGATING FUNGI-PHYCOMYCETES

of their favourite host. Thus, by asexual reproduction during the summer, and by hybernation of the oospores through the winter, provision is made for the continuance of the species. Incidentally, it may be observed that in one genus, that of *Cystopus*, the habit of the parasites is but little like that of the residue of the *Peronosporaceae*: the conidiophores are extremely

short and simple, and the conidia are produced in chains; but the sexual reproduction by oospores is virtually the same, and this is almost the only link which unites them. It is worthy of remembrance here that there is manifest in this group a gradual loss of sexuality, although external features remain much the same.

The Saprolegniaceae, from their aquatic habit, would at first seem to have an affinity with Algae, rather than with Fungi, but this is rather analogy than affinity. The hyphae, in most cases, are modified at their extremity, and become zoosporangia, are elongated cells which separated from the rest of the hypha by a septum (Fig. 108). After the zoogonidia have escaped through an opening at the apex, the hypha, or stem, continues to grow up through the empty sporangium, and



FIG. 108.—Sporangia and zoospores of Saprolegnia.

forms a second sporangium, and this, in like manner, when the zoogonidia are discharged, may enclose a third, so that upon old threads it is not unusual to see the remains of two or three empty sporangia, the one within the other. The zoogonidia are produced in great numbers, in each zoosporangium, having

the common ovate form, with a pair of active cilia at the smaller end. At maturity they escape by an orifice at the apex, and swim freely and actively in the surrounding water. In addition to this asexual reproduction, there is a more complex system of sexual reproduction, by means of antheridia and oogonia, the resultant oospores, or resting spores, serving to carry the germs through the winter and provide for their appearance in the spring. In typical species the sexual apparatus is of this kind, the oogonia are globose cells, generally terminal on short branches of the mycelium (Fig. 109). The external membrane is absorbed at various points, leaving it



FIG. 109.—Oogonium with two oospheres of Achlya. After De Bary.

pierced with rounded holes. The protoplasm becomes divided into a greater or less number of distinct portions, which become rounded into little spheres and separate from the walls of the cell to congregate in the centre, where they float in a watery fluid. During the formation of the oogonium, there arise from its pedicel, or the neighbouring filaments, thin curved branches, which are sometimes twisted round the pedicel, but tend towards the oogonium. Their free extremity is closely applied to the

wall, and becomes slightly inflated above, and cut off below by a septum. It is then an oblong cell, or antheridium, filled with protoplasm. Each oogonium possesses one or several of these antheridia. Towards the time when the oospheres are formed, each antheridium projects into the interior of the oogonium one or more tubular processes, which are applied by their extremities to the nearest oosphere. They have not been seen to open, nor has anything like a discharge of protoplasm been observed. Afterwards the oospheres become covered with cellulose, and are converted into so many oospores. When they have arrived at maturity these oospores possess a tolerably thick integument, which is double, and, after a considerable period of rest, they develop germ tubes or sporangia direct.

The Entomophthoraceae are minute parasites which inhabit the bodies of small flies and other insects, and are "distin-

CONJUGATING FUNGI—PHYCOMYCETES 235

guished by the production of numerous hyphae of large diameter and fatty contents, which ultimately emerge from the host in white masses of peculiar appearance, producing at their extremities large conidial spores, which are violently discharged

into the air and propagate the disease. In addition to these conidia, the propagation of the fungus, after long periods of rest, may be provided for by the formation of thick-walled resting spores,



adapted to withstand successfully the FIG. 110.—Hyphal bodies. most unfavourable conditions. These After Thaxter.

resting spores, which may be either sexual (*zygospores*) or asexual (*azygospores*), finally germinate and produce conidia that are discharged in the usual fashion, and serve to infect fresh hosts."¹

Infection results from contact of one of the conidia which adheres to the surface of the host, germinates there, and the



FIG. 111.—Conidiophores of Entomophthora. S.P.C.K.

germ-thread enters the body. After entering, growth proceeds rapidly and forms "hyphal bodies" (Fig. 110), which are short thick fragments of variable size and shape, continually reproduced by budding, until the body of the host is more or less completely filled with them. Having absorbed the contents of the body, these hyphal bodies germinate, each one producing one or more threads, which proceeds directly into the outer air, and bears its conidia, or it branches indefinitely, each branchlet producing spores at the extremity (Fig. 111). These are the conidiabearers, and their results the simple asexual reproduction. Conidia are formed by constriction or budding,

and when fully matured are forcibly ejected to a considerable distance. The discharged conidium germinates at once, but,

¹ Thaxter On the Entomophthoreae of the United States, 4to, 1888.
failing to reach a suitable host, a secondary conidium is formed, resembling that from whence it was derived (Fig. 112). Should this second fail in finding a suitable host, a third is formed from the second in the same manner.

The other form of reproduction is by means of resting



FIG. 112.—Secondary spores of Entomophthora. S.P.C.K.

spores, which may be sexual or asexual, and proceeds also from the hyphal bodies. The latter, or azygospores, are formed by the conversion of a hyphal body into a resting spore, or by direct budding therefrom (Fig. 113). They are usually spherical, rather large, surrounded by triple walls. Sexual resting spores, or zygospores, are produced as the result of conjugation of opposite threads. Threads either within or without the body of the host produce lateral outgrowths, at opposite points of two different threads, which meet midway and coalesce. The intermediate walls are absorbed, a connective is

formed, and the contents are mingled. A bud is produced upon

the connecting canal, which appropriates the contents of the two conjugating cells, and the zygospore is formed. After this the empty hyphae disappear. Rarely another modification of conjugation takes place. The hyphal bodies join laterally, by means of short processes, and produce an expansion at the point of union, which enlarges and absorbs the contents of the two conjugating bodies, and thus a resting spore, or zygospore, results. Some other slight modifications take place, according to the species, but the general character is



FIG. 113.—Conjugating hyphal bodies. Thaxter.

the same (Fig. 114). The mature resting spores are spherical,

CONJUGATING FUNGI-PHYCOMYCETES

smooth, slightly coloured, but their ultimate history and development are still rather obscure.¹

By comparison of this family with the preceding it will be observed that whilst the gonidial reproduction resembles most that of the Peronosporaceae, it is by no means the same : the gonidiophores are less highly developed, and active gonidia, or zoogonidia, would seem to be absent. The conjugation also differs from that of all the other families, and approaches more closely to that of the Algoid type, as represented by some of the filamentous Conjugatae.

From this summary of the main features of the four

normal families, we must turn to the two remaining families, which are so far abnormal, or aberrant, as to be deficient of conspicuous hyphae. The Chytridieae are mostly very minute, and either parasitic or saprophytic, forming sporangia of characteristic forms, the contents breaking up into swarm-spores. These zoogonidia, or swarm-spores, escape from the sporangium, through a narrow opening, usually at the apex. Nowakowski² has given the life-history of one species, which is parasitic upon In this species of Poly-Euglena. phagus, the swarm-spore, when it has FIG. 114.-Conjugating hyphae come to rest in the water, becomes spherical in shape, and at once puts



in Entomophthora, with zygospores. After Thaxter.

out hair-like, tubular rooting (rhizoid) processes in indefinite directions. If one of these encounters a resting Euglena it penetrates into its body, destroying and exhausting it to supply food to the parasite. The parasite then begins to increase in size, the tubes become larger and thicker, and new ones are formed which throw out branches, and attack and destroy any new Euglenae which they encounter.

¹ Vegetable Wasps, etc., by M. C. Cooke, 1892, p. 10.

² Beitrag zur Kenntniss der Chytridiaceen, von Dr. L. Nowakowski, Breslau, 1876.

In this way a much-branched plant is formed, with hair-like terminal branchlets, which connect with the larger main stems, and through these with the body of the original spore; the latter has grown in the meantime into a large round or elongated vesicle at the expense of the Euglenae, which have been exhausted by the rhizoids. When it has reached a certain size, varying according to the food which has been supplied to it, it shows itself to be a sporangium. It grows out at one spot into a bluntly and irregularly cylindrical thick tube with a delicate membrane, into which the whole of the protoplasm passes, and is at once divided into swarm-spores. This process of development may be repeated for many generations, and leads to an immense multiplication of individuals, if there is a sufficient number of Euglenae within reach. When this has taken place, the course of events changes. The young plants remain for the most part small and become gametes, which conjugate in pairs, each pair forming a zygospore, and these behave as resting spores. Of the two conjugating gametes, the one which is the supplying gamete has usually a round and larger body, but shows no other apparent difference before contact with the other, the receptive gamete. The latter usually continues to be smaller, and often very small, and puts out rhizoid branches, and if one of these encounters a supplying gamete it applies its extremity to it as a conjugating tube, and increases in thickness, while it ceases to grow in length. The membrane between the conjugating tube and the supplying gamete disappears at the point of attachment, and an open communication between them being thus established, the whole of the united protoplasm of both gametes passes into an enlargement of the conjugation tube, close to the point of attachment; the swelling gradually expands into a spherical vesicle, and, being delimited by a membrane after receiving the protoplasm, becomes a thick-walled zygospore. The outer wall assumes a pale yellow colour, which is in some cases smooth, in others spinulose. The whole process of forming a zygospore is completed in from six to seven hours. This zygospore is a resting spore, and germinates when its period of rest is over, producing a zoosporangium like non-conjugating plants.¹ The

¹ British Fungi-Phycomycetes, etc., by G. Massee, London, 1891.

CONJUGATING FUNGI-PHYCOMYCETES

genus Synchytrium is provisionally included in this family, although no sexual reproduction is known. When compared with such families as the *Mucoraceae* and the *Peronosporaceae*, the *Chytridieae* seem to have little in common, save the phenomenon of conjugation, and appear to be, in fact, in conjunction with *Protomyceteae*, an outside group, of doubtful natural affinity.

In the *Protomyceteae* the mycelium is very fugitive, at first seated in the tissues of the plants upon which the species are parasitic, and then septate, contrary to the usual condition in the *Phycomycetes*. Conidia are unknown. The entire system of reproduction consists in the development of thick-walled resting spores. In germination the endospore escapes through the rupture of the thick wall, in the form of a sporangium, filled with minute, motionless spores, which conjugate in pairs. After conjugation the spores germinate by emitting a slender germ-tube, which enters the foster-plant, and produces a mycelium, from which resting spores are developed, and the cycle is complete.

Strongly impressed with the absence of any true natural affinity between the last two families and the four preceding ones with which they have been associated, we have no alternative but to include them under protest, and to suggest that the one fact of conjugation, as feebly carried out, is insufficient, in the absence of other indications of relationship, to warrant the retention of these two families with the *Phycomycetes*. As evidence that their affinities have always been held in doubt, it may be added that, until very recently, the genera Chytridium and Synchitrium have been included with Algae,1 although subject to the observation that "The genus Synchitrium appears to be more nearly related to Protomyces, amongst Fungi, than to Algae." Under any circumstances they can only be regarded as aberrant families, mechanically and provisionally tacked on at the end of this order, until they may be assigned to a more fitting place.

¹ British Fresh Water Algae, by M. C. Cooke, 1884, p. 198.

239

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241

CHAPTER XX

RUST FUNGI-UREDINEAE

NONE of the primary groups in the division of Fungi, as adopted by Fries, were so unsatisfactory as that of the Coniomycetes, which included with the Sphaeropsideae and the Melanconieae such heterogeneous elements as the Uredineae and the More recently the two latter were combined Ustilagineae. under the name of Hypodermeae, and might still be so retained without grave objection, although they have little save their parasitism in common. One of the most important divergences is to be found in the complex character of the fructification in the Uredineae, as compared with the comparative simplicity of The species form erumpent pustules that in the Ustilagineae. on living plants, being furnished with an innate septate mycelium, but destitute of perithecia or true asci. The typical fructification consists of spermogonia, aecidia, uredospores, and teleutospores. The Spermogonia usually accompany the Aecidia, and are punctiform, yellow, orange, brown, or turning black; the sporules are very small, and ovoid or cylindrical, mostly expelled from a pore or orifice, at the apex of the pustule, in little tendrils. The Aecidia are pale, and possess a pseudoperidium, mostly in the form of a little cup, when mature, with a serrate white margin, popularly termed " cluster-cups" (Fig. 115). The aecidiospores are simple, rather large, usually orange and warted, produced in chains within the cups, or pseudoperidia. The uredosporiferous sori are variously coloured, rarely possessed of a pseudoperidium, and mostly The uredospores are continuous, subglobose, and pulverulent. hyaline, yellowish, or pale brown, very rarely catenulate, rather large, germinating from two to six pores externally, and for

RUST FUNGI-UREDINEAE

the most part aculeolate or minutely punctulate. The *teleuto-sporiferous sori* are also variously coloured, and very rarely furnished with a pseudoperidium. The *teleutospores* are either

continuous or septate, generally supported on a persistent peduncle, externally smooth, or ornamented in various ways by spines, warts, granules, or other appendages, germinating through determinate pores. By germination of the teleutospores a



FIG. 115.—" Cluster-cups" of Aecidia.

promycelium is developed, which is typically four-septate, bearing sporidiola at the apices of sterigmata. This, therefore, is the normal sequence of fructification—spermogonia, aecidia, uredospores, teleutospores, and sporidiola—but some one or more of the series is often suppressed.

The arrangement adopted most generally is, to a great extent, an imperfect one, since it assumes a knowledge of the most important features in the life-history of each species. This may be all very well for a local flora, where details may be determined, but it is of doubtful value in dealing with a mass of exotic species, where special information is not to be obtained. It is an open question whether all sound classification should not be based upon characters which may be determined directly from the individuals themselves, and should include nothing which is not present or evident in examples of any given species. The entomologist finds no difficulty in classifying his Lepidoptera, although they may have passed through previous stages wholly different from that presented by the imago, and his classification is based upon features to be found in the perfect insect, and in those alone. Is it so with the species of Puccinia, for example? if recent disclosures are to accepted. There is a certain species called Puccinia phragmitis, which is found growing upon Phragmitis communis; and there is a second supposed species called Puccinia Trailii, which occurs upon the same host; and there is still a third species which has been named Puccinia Magnusiana, having the same How are these species proposed to be distinguished, habitat. except by the intuitive knowledge that the Aecidium of Puccinia phragmitis is supposed to flourish on the leaves of

certain species of Rumex, that of Puccinia Trailii on Rumex acetosa only, and that of Puccinia Magnusiana on Ranunculus. repens and bulbosa. If the Puccinia itself, which corresponds, to the imago stage, in being the ultimate and most perfect. development of a cycle-is insufficient for the determination, or discrimination, of Puccinia phragmitis, Trailii, and Magnusiana, then it may be contended that the basis of classification is greatly defective for all practical purposes. Yet it is not uncommon to meet with observations associated with one species, so called, of *Puccinia*, that "it cannot be distinguished morphologically" from another species, but that "its life-history is different." This is the crucial test of the system, for if the perfect stage of one species is not to be distinguished from another, or, it may be, from two others, although the system may be very philosophical, it is nevertheless impracticable. Let us proceed, however, to the method set forth in Saccardo's Sylloge, and now generally adopted.

The primary divisions are again based upon the spore and its septation. The Amerosporae includes all the genera in which the teleutospores are unicellular. Of these, two genera have no pseudoperidium to enclose the teleutospores, namely Uromyces and Hemileia. The latter is represented by the destructive coffee-leaf disease, the assumed teleutospores of which have half the surface smooth, and half warted. Its association here is scarcely more than provisional. Uromyces the great genus of the section, and the teleutospores is germinate by one pore. In typical species the spermogonia, aecidia, uredospores, and teleutospores are all present on the same host-plant. In others the spermogonia and aecidia are unknown. In another section the spermogonia, aecidia, and teleutospores are present on the same host, but the uredospores are unknown. In the final section only the teleutospores are known, the spermogonia, aecidia, or uredospores never having been discovered or recorded; this is, in effect, the section which includes the imperfectly known species. The two genera in which the uredospores are included in a pseudoperidium are Melampsora and Melampsorella, very closely related-the sori of the teleutospores being crust-like, blackish, and determinate in the former; flattened, indeterminate, and pallid in the

RUST FUNGI-UREDINEAE

latter. In the one remaining genus of the section, that of *Cronartium*, the teleutospores surround a vertical columella, but in external appearance the species resemble Uredines as little as possible, and are not unlike persistent tendrils of some member of the *Melanconieae*.

The *Didymosporae* are well typified by the large and important genus *Puccinia*, with its transversely septate teleutospores. The grades are like those of *Uromyces*, viz. spermogonia, aecidia, uredospores, and teleutospores; but a different element comes into the subsidiary grouping, since it is contended that in some cases these grades are not all passed upon the same host. It is perfectly true that in one typical group,



FIG. 116.—Section of aecidia and spermogonia. S.P.C.K.

that of the Auto-pucciniae, all the grades are developed on the same species of plant; but in the Hetero-pucciniae, although all the same grades are affirmed to be present, yet the spermogonia and aecidia appear on one species of plant, generally a Dicotyledon; whilst the uredospores and teleutospores make their appearance on a plant belonging to quite a distinct genera of plants, mostly a Monocotyledon. Now the doctrine which associates these forms is that designated Heteroecism, and although some writers contend that the facts are not effectually proved, and therefore dispute the conclusions, others accept the inferences derived from artificial cultures as conclusive, and bow down to Heteroecism. Whichever may ultimately succeed in persuading the rest, it is manifest that Heteroecism for the present is the favourite, and consequently the faithful are happy in finding the four grades separated, two on one kind of matrix and two on another. To quote a very familiar example, the spermogonia and aecidia of the berberry are found

developed on Berberis vulgaris, but no corresponding uredospores or teleutospores upon that plant, and therefore they



FIG. 117.-Aecidiospore in germination. After Tulasne.

have to be sought elsewhere (Fig. 117). On the other hand, the uredospores and teleutospores of Puccinia graminis flourish on wheat and other grasses, whilst no spermogonia or aecidia have been known to infest the latter plants. Hence it is concluded that the above form the normal series. with the spermogonia and aecidia on the berberry, and the uredospores and teleutospores on wheat, which completes the cycle. This theory is supported by the contention that the germinating spores of Aecidium berberidis are capable of producing Puccinia graminis by artificial inoculation on wheat: and conversely the promycelial spores of

Puccinia graminis (Fig 118) may be used to inoculate the leaves of the berberry, and produce thereon

Aecidium berberidis. This is the theory and its application, which we will here leave as it In another group, the stands. Brachy - pucciniae, spermogonia, uredospores, and teleutospores are found on the same species of plant, but the aecidia are unknown. To this succeeds the Hemi-puccinia, in which uredospores and teleutospores occur on the same plant, but the spermogonia and aecidia are unknown. It is here that the Puccinia sceptics would place graminis were they not debarred FIG. 118. - Puccinia teleutospore by the anathemas of the votaries of Heteroecism. Hereafter follows



germinating and producing promycelial spores. After Tulasne.

the group Pucciniopsis, in which spermogonia, aecidia, and teleutospores have been recognised, but not uredospores, so that in this group of species the uredo stage is deficient. Of the two remaining groups, Micro-pucciniae includes those

RUST FUNGI-UREDINEAE

species in which only teleutospores are known, and these do not germinate for a long time after the foster-plant is dead; and the Lepto-pucciniae, in which also the species only possess teleutospores, but the sori are compact, and germination takes place at once and whilst the foster-plant is living. Of course, outside of all these groups there still remain a rather large number of species, of uncertain place, mostly with only the teleutospores definitely known, but which it is suspected will ultimately find a place in some of the foregoing groups, when their life-history has been ascertained. Other Didymosporous genera are Uropyxis, which seems to be hardly generically distinct, in which the teleutospore is involved in a thick permanent hyaline integument; and Diorchidium, which differs chiefly from Puccinia in the septum being vertical. Gymnosporangium is most distinct in the teleutospores being agglutinated together in, generally, large tremelloid masses, the teleutospores themselves being transversely uniseptate, or very rarely biseptate, nearly hyaline, with long, sometimes very long, pedicels.

In Phragmosporae the teleutospores are three, or more,

septate, in one direction. In most genera they are destitute of a pseudoperidium, whilst in Phragmidium¹ (Fig. 119) and Xenodochus the uredospores are solitary. The differences between these two genera are slight: in the former the teleutospores are cylindrical, the cells not readily breaking up into joints; in the latter the cells are more numerous and moniliform, soon breaking up into the component cells. In two genera the uredospores are catenulate, of which Coleosporium is the most important; in this genus the uredospores are associated in chains, and the teleutospores FIG. 119.-Teleutospores are three, or many, septate. The pro-



of Phragmidium.

mycelium is continuous. In Chrysomyxa the uredospores are as in Coleosporium, the teleutospores are multiseptate, and simple or

¹ Hamaspora longissima has been included under Phragmidium, but we doubt if it should not be maintained as a distinct genus.

branched, whilst the promycelium is triseptate. In three small genera the teleutospores are longitudinally septate; that is, in *Pucciniastrum*, in which the uredospores are enclosed in a pseudoperidium, but the teleutospores are evolved externally to the matrix; *Thecopsora*, in which the uredospores are also enclosed in a pseudoperidium, and the teleutospores are intracellular; in *Calyptospora* there are aecidia but no uredospores, and teleutospores, provided it is accurately determined that, in the single species, the aecidium is found on the leaves of *Abies*, and the teleutospores are enclosed in a pseudoperidium— in *Endophyllum* resembling an *Aecidium* with catenulate spores; and in *Milesia* the teleutospores are catenulate within a reticulate immersed pseudoperidium. These two genera are outsiders and only remain here on sufferance.

The *Dictyosporae*, in which the teleutospores are transversely, longitudinally, and obliquely septate, contain but two very distinct but different genera. In *Triphragmium* the teleutospores are triseptate, or radiately three-celled. In *Ravenelia* the teleutospores are many-celled, the cells radiating or concentric, often with hyaline basal cells, in surface aspect resembling the glomerules of *Sorosporium*.

In such an arrangement as the foregoing, wherein so much depends upon a knowledge of the life-history of every species, it is but natural to expect that there will be a number of forms which present the earlier stages of a succession, and are yet deficient of the requisite determinator, the teleutospore. These have to be relegated to outside groups under the denomination of Inferior Uredines, or Imperfect Uredines, and as such find their places under the following genera. The species having spermogonia only are ranged under Aecidiolum-the species of Aecidium, which remain isolated, retain their position under that old generic name; the species which are analogous, but have elongated pseudoperidia, and were formerly known as Raestelia, still retain that name, producing aecidiospores, as also does Peridermium, which is analogous to Aecidium, on conifers. The remaining genus is Uredo, which includes all unplaced species of uredosporous Uredines, whether known formerly as Uredo, or Trichobasis, Lecythea, or Caeoma, the latter having the

spores catenulate. Here, then, we have the spermogonia, aecidia, and the uredospores, which may possibly prove to form parts of unknown cycles, the position, affinity, and association of which must be left to the chances of future investigation.

During late years there has been no lack of investigation and observation on the structure, growth, and development of the Uredines, which have mostly taken the form of artificial cultures. Whether the same results take place, and in precisely the same manner, in a state of nature, cannot be affirmed, whilst some present grave reasons for doubt. It is still possible that, When if the facts are accepted, the inductions may be wrong. it is argued that certain experiments succeed in producing upon certain plants the identical Uredines which would have been developed in the ordinary course of nature, a sceptic will naturally inquire for the evidence which proves that the resulting Uredines were really produced by inoculation, or whether the elements were not already present, and that these were simply stimulated by the introduction, or intervention, of other agencies, and hence not actually produced by inoculation. Common sense would allow that, if the resulting Uredine were foreign to the particular species of plant, the assumption of inoculation would be more convincing. This is not the place to enter upon a discussion of the doubts and dangers which attach to inductions from the results of artificial cultures, hence it must suffice to suggest that such doubts and dangers may still continue to exist in the minds of those who venture to hold independent opinions.

Suggestions have not been wanting of sexuality, or of fertilisation which implies sexuality, in the Uredines. The application of the term "spermogonia" to the small pustular eruptions, which occupy the first place in the cycle, can scarcely be accepted as a suggestion, but some authors have assigned to the minute spore-bodies not only the name but the function of spermatia. Meyen was evidently of this opinion, and he was not the only one who thought that they played the part of the male element. Worthington Smith has intimated that he has often seen the small sporules attached to the exterior of Aecidiospores, but he was unable to trace any pollinial tube into the interior. Against the supposition that they are fecundative

bodies it may be urged that the globose form, and absence of movement, are unusual with known spermatia. And again, the fact of their power of germination, or rather of budding, is opposed to their possessing the function of spermatia. Cornu found that the so-called spermatia budded in the manner of Saccharomyces. In saccharine solutions they behave in a very similar manner to yeast spores, or analogous to the concatenate production of cells in the Ustilagineae.

It has also been suggested that in the aecidium stage the conjugation of two swollen hyphae of the mycelium takes place, from which the whole aecidial cup is produced as the result of a sexual act. This again requires careful confirmation before it can be accepted as more than a hypothesis. In the subsequent stages of uredospore and teleutospore no sexual act has been discovered, and at present we are bound to admit that in the Uredineae sexuality has not been proven.

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CHAPTER XXI

SMUT FUNGI-USTILAGINES

IT was at one time so customary to associate the Ustilagines with the Uredines that it would have been thought that some close bond of union existed between them, instead of which they have really no closer affinity than the fact of their being alike parasites upon living plants. In the days when the Coniomycetes were accepted as an order of Fungi, on the basis that they produced spores, on more or less distinct sporophores, with the threads, or hyphae, obsolete, or nearly so, then the Ustilagines and Uredines were associated with the Sphaeropsideae as members of that order. It was then contended that this division was distinguished "by the vast predominance of the reproductive bodies over the rest of the plant, if not in size, at least in abundance, and from the ease with which in general they fall from the point of attachment, in consequence of which, as the name implies, they have a dusty appearance, and often soil the fingers of those who handle them."1 No longer can so artificial an association be recognised, and whilst the Sphaeropsideae hold lower rank as imperfect forms, the two groups of Ustilagines and Uredines maintain independent positions, as autonomous, within certain restrictions. Tulasne contributed much to the better knowledge of the Ustilagines in 1847, to which Fischer de Waldheim, with Brefeld and others, have contributed since. How far these organisms differ from the Uredines must be gathered from a comparison of the present with our chapter on the latter group.

It must be premised that these are pustular Fungi, which

¹ Introduction to Cryptogamic Botany, by M. J. Berkeley, London, 1857, p. 315.

attack growing plants, and produce copious soot-like spores, so that they have acquired the general name of "Smuts." The mycelium is deeply seated in the tissues, and the spores are developed in definite positions on the host: on the stem, leaves, flowers, ovaries, fruit, and sometimes in the corm, tuber, or root, but seldom in more than one of these places, and that one habitual to the species. A good example may be seen in the smutted ears of corn, or the distorted receptacles of the goat's-beard.

The mycelium is an important element in this family, although so delicate and deeply seated that it is often passed over. The whole substance of the host may be penetrated and taken possession of by the mycelium before there is any external evidence of its presence; therefore when the pustules are formed it is too late to apply remedial measures, for the plant has long been doomed. It is always tedious and difficult to trace the ramifications of mycelium in growing tissue, but in some of these species it may be seen bearing haustoria or suckers amongst the cells. Not only does the mycelium traverse the intercellular spaces, but frequently the branches pierce the walls of the cells, and though seen most readily in young plants, it is always manifest about the spore-pustules. The persistency of the mycelium is one of the agencies by which the continuity of the species is preserved. When the foster-plant dies in the winter the mycelium dies with it, but when the root-stock is perennial the mycelium also remains, to revive and penetrate the young shoots which are put forth in the spring. All the leaves of the violet may die year after year, and still every season Urocystis violae appears again, even when every infested leaf has been picked and burnt.

The most important function of the mycelium in this family is its concern in the formation of the fruit. At the special spot where the development of fructification is to take place the mycelium undergoes some change in its character : the walls increase in thickness, and the contents become gelatinised. Some slight modifications take place in the different genera, but for the most part the hyphae branch and become entangled so as to form compact knots, or spore-beds. With this the hyphae gradually swell in places, and it is evident

SMUT FUNGI-USTILAGINES

that a change is taking place within. The swellings are indication of spore - formation, which proceeds sometimes centripetally, so that those on the exterior are most completely developed, the circumference darkens, and an epispore is formed. In Sphacelotheca part of the hyphae are concerned in the production of the receptacle and columella, and part in the origination of the spores. In some genera the production of spores is centrifugal, and the peripheral spores are sterile. In Sorosporium "the spore-forming hyphae from several contiguous mycelial branches incline together and twist themselves into a ball, as happens in the formation of a Lichen These convoluted and contorting spore-forming thallus. hyphae, being gelatinous, soon become so entwined and entangled that they cease to be individually recognisable; to all appearances they coalesce together in part, if not entirely, and on the exterior of this gelatinous ball other hyphae are seen encircling it. These latter also being gelatinous, soon lose their individuality, although at times traces of their concentric arrangement can be made out. Spore-formation takes place only in the central gelatinous ball, in the middle of which it commences by the central part darkening in colour and becoming differentiated into spore-like bodies, which vary in number from four to sixteen. Apparently these bodies again subdivide, so that when the spores arrive at their maturity the spore-balls contain sixty to a hundred or more spores. In the young state the developing spores are polygonal from mutual pressure; subsequently the balls increase in size, and the gelatinous zone swells also. When the spores assume their dark brown colour the gelatinous zone begins to be absorbed, and entirely disappears when the spores are fully matured. In a certain sense the spore formation is centrifugal, as it commences in the centre of the gelatinous ball, but the peripheral spores are the oldest, having been pushed outward by the formation of younger spores in the centre."1

The spores of the Ustilagineae are practically teleutospores, and are called such by some writers. They are composed of two membranes—the outer, or exospore, the thicker and dark coloured; the inner, or endospore, thin and colourless. ¹ British Uredineae and Ustilagineae, by C. B. Plowright, London, 1889, p. 64.

253

The surface of the epispore varies in its character, being sometimes quite smooth, in other species reticulated, in others so minutely granular as to appear to be smooth until closely examined, or in others distinctly rough and either obtusely warted or spinulose. In colour they seem to be black in a mass, but viewed obliquely sometimes with a yellowish or olive tinge; seen under the microscope, by transmitted light they may be black or brown, violet, olive, or yellowish, and rarely hyaline. Where colour is present it resides in the epispore, and is fairly constant in each species when mature.

The form is commonly globose, or approximately so, when perfectly free, but being usually closely compressed in growth, is apparently angular. The spore-masses in some genera, such as Ustilago and Tilletia, are more loosely packed, and the teleutospores do not adhere to each other in definite clusters, but are normally free. In Sorosporium and Thecaphora they form compact clusters, which in the latter genus separate with difficulty, whilst in Cintractia, although at first agglomerated, In Urocystis there are a few large, darkthey soon separate. coloured fertile spores, closely adnate to each other in the centre, and these are surrounded by hyaline sterile cells, or pseudospores, which give the appearance of a beaded border. In Entyloma, Melanotaenium, and Entorrhiza we meet with aberrant genera, which remind us of Protomyces and Synchytrium, and are probably more closely allied to the latter than they are to the rest of the Phycomycetes.

Germination of the teleutospores in this family has often been observed and watched. In some species a small germpore has been observed, but they are never so distinct as in the *Uredineae*. When the spores germinate they protrude a germ-tube—usually designated, for reasons hereafter evident, a promycelium. In a certain sense it may be regarded as analogous to the protonema of mosses. This promycelium bears small hyaline bodies, which resemble spores, and are called by Continental mycologists *sporidia*, a name to which we take exception as it should be restricted to spores generated in asci. We will call them, for the time, promycelial spores, as suggested by Plowright, and much more appropriate. The promycelial spores will bud and produce secondary promycelial spores,

SMUT FUNGI-USTILAGINES

and these again may continue to multiply themselves many times by budding, after the manner of yeast-spores, which is the term applied to them by Brefeld, but liable to misinterpretation. In order the better to comprehend the process, it may be detailed as observed in *Tilletia* (Fig. 120). This parasite produces its teleutospores within the grains of wheat, and is

known to farmers as "bunt." The appearance of the grains very little externally is changed, but slightly darkened in colour, and when crushed are seen to be filled with a sooty, rather fetid powder. These teleutospores are globose, dark coloured, almost black, and the surface minutely reticulated. When placed in water they germinate in about forty-eight hours. A germtube is emitted from a very small germ-pore, but it does not attain any considerable length; and this germ-tube constitutes the promycelium, into which the contents of the parent spore pass and retreat





to the extremity, and are shut off by the formation of a transverse septum. Tuberculations are soon manifest about the summit, and these by lengthening become the first promycelial spores. They are thread-like, curved, and colourless, to the number of from four to a dozen. When fully developed they are cut off from the promycelium by a septum at the base. Soon afterwards these primary spores will be seen to connect themselves, mostly in pairs, by a transverse connective, performing an act of conjugation. These conjugated primary spores are often separated from the promycelium, but they may remain for a long time attached. In due time budding takes place, and the buds become converted into cylindrical curved secondary spores, the

second generation of promycelial spores, which in like manner are cut off by a septum at the base, and become free independent bodies. The act of conjugation, which results in their production, is not an essential, because solitary primary spores are equally capable of budding and producing secondary spores, although they are usually smaller than those produced by conjugating primary spores. Hence it may be concluded that the conjugation of the linear spores is not a sexual act. The secondary spores are usually those which, by germination, enter the host-plant and form a mycelium, but they are also capable of budding and forming promycelial spores of a third, or even of a fourth, generation, if the conditions are unfavourable for infecting a new host-plant.¹

The germination in Entyloma is similar to the above, but less complex. The spores send out a germ-tube in about twenty-four hours, and this constitutes the promycelium, which develops several branches at the apex, each of which is cut off by a septum at the base and becomes a promycelial spore. These spores then conjugate in pairs by the formation of a connective bridge; afterwards, by a continuation of growth at the apex, secondary spores are produced, which fall off and germinate. The growing point enters the host-plant and forms a mycelium, which starts a new infection, and in course of time teleutospores of a normal kind are developed in In this genus conidia are also produced direct from clusters. the mycelium, the conidia-bearers rising to the surface of the leaf through the stomata. These conidia germinate on the surface of the leaf upon which they fall, and the germ-tube enters the stomata and forms a mycelium. They are able to form secondary conidia, but this seldom takes place under normal conditions. Hence there are two forms of reproduction in this genus—that of the germinating teleutospores, forming a promycelium which gives rise to promycelial spores, and these after conjugation developing secondary spores, capable of reproducing the parasite, after an alternation of generations; and, secondly, of germinating conidia, which reproduce the parent Entyloma at once, without an intervening generation.

¹ "On Bunt Spores," by M. C. Cooke, Journal of Quebett Microscopical Club, vol. i. p. 167, 1868.

SMUT FUNGI-USTILAGINES

The teleutospores in some instances in this family are resting-spores—that is to say, they are capable of germination after a period of rest; but for the most part they germinate freely when moist, and a delay of germination can only be secured by maintaining a condition of dryness which does not obtain in a state of nature. It is uncertain how the interval is connected between the maturity of the teleutospores and the growth of the seedling hosts, where the entire plant is annual. In the case of perennial hosts a persistent mycelium removes all difficulty, but where mature teleutospores are produced upon an annual in summer or autumn, and there are no seedlings until two or three months afterwards, it is not evident how the continuity of the species is preserved.

It has been shown that, when cultivated in a suitable medium, the promycelial spores multiply themselves almost indefinitely by budding, but the nutrient fluid must be maintained unexhausted. In this condition the growth is similar to that of yeast, and the term "yeast cells" has been applied to them. So long as the supply of nutrient fluid is maintained there is no departure from the budding process. Brefeld maintains it to be extremely probable that the conidial fructification, in a toruloid form, occurs in nature in many species of the Ustilagineae; that they have the power of propagating outside the host as "torulae," and develop their spore fructification only when they penetrate the tissues of the hostplant by means of germ threads, which takes place when the supply of nutriment ceases. The extreme assumption on this basis is that certain forms of Saccharomyces, or indistinguishable therefrom, are in fact aquatic forms of the conidia of Ustilagines, which have become "toruloid" on account of their surrounding conditions. In fact, that some ferments are not autonomous, but depraved Ustilagines which have abandoned their parasitic habit and become saprophytes.

It will therefore be evident by this time that the members of this family are universally parasitic, and that the hosts are herbaceous plants. In a great number of instances the graminaceous plants are the victims, but by no means exclusively. In all cases they are eminently destructive, and, from their habit, difficult to contend with. Most of the pro-

257

posed remedies are preventive and not curative; they could hardly be otherwise until that period in their life-history is more definitely determined which intervenes between the maturity of the teleutospores and the inoculation of seedlings of the host-plant.

Assuming the total of known species to be somewhere about three hundred, upwards of one hundred of these affect the grasses, and nearly fifty attack other Monocotyledonous plants, so that scarcely half of the total are found on Dicotyledons. This is a peculiar fact in distribution which is perhaps without parallel in any other family of the parasitic Fungi.

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CHAPTER XXII

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE

In the old arrangement by Fries, one of the primary divisions of Fungi was that termed *Coniomycetes*, which was interpreted as "Dust-fungi," and was represented as including those fungi in which the spores were the principal feature, such spores appearing like an impalpable dust. It was, perhaps, an odd mixture, but this group included not only the *Sphaeropsideae*, as at present limited, and the *Melanconieae*, which are closely related, but also the *Uredineae* and the *Ustilagineae*, which are not related at all, and are now separated and rank as a distinct group. It need not be explained here wherefore the *Uredineae* and its allies were entirely out of place in an association with Fungi which either possessed a distinct perithecium, in which the spores were generated, or a pseudoperithecium formed from the matrix.

The group now under consideration is analogous, in external features, to the *Pyrenomycetes*, but wholly deficient of asci. The perithecia, or pseudoperithecia, include only stylospores, and have been assumed to be imperfect representatives, or imperfect stages or conditions, of the *Pyrenomyceteae*, and hence called "imperfect capsular Fungi." In some instances this may be undoubtedly true, but we think it assuming too much to affirm that *all* are imperfect conditions of higher Fungi, because it has been demonstrated to be the case in a comparatively few instances. It is at least premature to decline acknowledgment of thousands of very distinct forms of Fungi in a systematic position, simply because a few of them have been shown to be transitional, whilst the majority may never be demonstrated to be other than autonomous. This

objection has been appreciated by Saccardo, who includes all the species in his Sylloge, although he relegates them to an inferior position as "imperfect fungi."

The Sphaeropsideae must be considered apart from the Melanconieae, on the fundamental basis that the former possess a distinct perithecium, and the latter are only circumscribed by a modification of the matrix. With this limitation, therefore, the Sphaeropsideae correspond to the Pyrenomyceteae, although dissevered by the absence of asci and paraphyses. It would be well if authors in future would respect Saccardo's definitions of the fruit in the different orders, by a restriction of the terms. Thus in the Ascomycetes, where the representatives of seeds, or the spores, as they are generally termed, are produced within asci, that they are sporidia. When produced naked on basidia, as in the Basidiomycetes or Myxomycetes, they should retain the name of spore. When enclosed in perithecia, but without asci, as in the Sphaeropsideae, then to be termed sporules. But when wholly naked, and without basidia, or receptacle, as in the Hyphomycetes, then to be termed The only modification to this arrangement which conidia. approves itself to us is the application of the term sporules to those bodies which are enclosed in a pseudo-perithecium, such as the Melanconieae, as well as those contained within a definite perithecium; and the restriction of conidia to absolutely naked fruit, in which there is neither perithecium nor semblance of a perithecium, as in the Hyphomycetes. Practically this means the association of the Melanconieae with the Sphaeropsideae, in the denomination of sporules, instead of union with the Hyphomycetes under the denomination of conidia. This may be a distinction of little importance, but it is one which appears to commend itself to consideration.

The Sphaeropsideae, therefore, may be thus defined, as Fungi possessed of a perithecium, but without asci, the sporules, or stylospores, being produced internally at the apex of more or less distinct supporting hyphae or pedicels, which, for the sake of distinction, should not be termed basidia, but sporophores. This would obviate any confusion with the spore-bearers of the Basidiomycetes, and the definition would be reduced to " perithecia, without asci, enclosing sporules, on more or less distinct

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE 261

sporophores." The primary families would depend for their distinctive characters upon the nature of the perithecium. The first and largest is the Sphaerioideae, in which the perithecia are membranaceous, coriaceous, or subcarbonaceous, typically subglobose, and closed; thus analogous to the old genus Sphaeria. The second family, Nectrioideae, with the perithecia similar in form, but fleshy or waxy, and usually brightly coloured, analogous to the old genus Nectria, or the more recent family Hypocreaceae. Then the third family, the Leptostromaceae, has the perithecium more or less dimidiate, and astomous, or with a longitudinal fissure, and black, corresponding in some respects to Hysteriaceae. Finally, the fourth family is Excipulaceae, with the perithecium cup-shaped, or patellate, at first spherical, then broadly open, and making the nearest approach to analogy with the Discomycetes. Each of these families we must therefore analyse a little more in detail, bearing in mind their distinctive family features.

The Sphaerioideae are therefore the Sphaeriaceous, or Sphaeria-like, Sphaeropsideae, with blackish closed perithecia; and although we should have preferred grouping them in a similar manner to our subfamilies of the Sphaeriaceae, we will rest content with the arrangement proposed in the Sylloge, which will be the one generally adopted for some time to come. Of course this method is an artificial one, to a great extent, being based upon the character of the sporules. The Hyalosporae is again the largest section, including all the genera with continuous hyaline sporules; those in which the perithecia are simple or distinct forming one subsection, and those in which the perithecia are composite or caespitose forming another. Amongst the simple species the larger number have the perithecia naked or smooth, and of these one genus, Phyllosticta, is often parasitic, growing upon leaves, the depressed and innate perithecia being grouped on discoloured spots; the remaining genera have the species not seated on definite spots, and of these three are very similar to each other; that is to say, Phoma, with the perithecia (Fig. 121) covered by the cuticle; Aposphaeria, with the perithecia exposed, or superficial, mostly on dead wood ; and Dendrophoma, which in all things else resemble Phoma except that the sporophores are

branched, instead of remaining simple. More recently the genus Phoma has been subjected to another mechanical subdivision into Phoma and Macrophoma, the latter to include all the species of *Phoma* which have sporules exceeding a definite



FIG.121.-Perithecium of sporules.

size, so that the determination of the genus may depend upon the difference of a micromillemetre. Another genus, Asteromella, which is equal to Asteroma, minus a subiculum, has the minute perithecia clustered on dendritic spots. There are five or six smaller genera, consisting of but a few species, which completes the series of genera Phoma with in which the perithecia are not rostrate. In Sphaeronema the habit is that of Phoma or

Aposphaeria, but the perithecia are rostrate. In addition to these follows a series of genera in which the perithecia are seated upon a subiculum of some kind, more or less distinct and definite. In Chaetophoma the perithecia resemble those of Phoma, but are innate in a dematioid subiculum resembling Fumago or Asterina. An allied genus, Asteroma, is the analogue of such genera as Asterina or Dimerosporium, the minute perithecia being seated upon, or amongst, a subiculum of radiating black fibrils. In the remaining two genera, Ypsilonia and Cicinnobolus, each contains but a single species, and the latter is parasitic upon Oidium. In the three genera which complete those in which the perithecium is bare, Neottiospora has the sporules cristate, and the other two genera have the sporules in chains. We pass now to the smaller series, in which the perithecia are hairy or bristly. Here are four genera, the most numerous and important of which is Vermicularia. In habit the perithecia resemble those of Venturia, or some species of Chaetomium, the long dark bristles are septate, and the sporules mostly curved. Pyrenochaeta is similar, but the hairs of the perithecium are shorter, and the sporules ovoid or oblong. Muricularia and Staurochaeta differ from the foregoing in the character of the external hairs. This brief review of the simple species leads us to the series in which the perithecia are composite or caespitose, usually Dothiorella resembles superficially with a definite stroma. either Botryosphaeria or Cucurbitaria. The pustules are

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE 263

erumpent, and consist of a number of perithecia aggregated Rabenhorstia, and especially Fuckelia, upon a basal stroma. have a subglobose stroma, in which are fertile cells, so that in habit and structure there is a similarity to some species of the ascigerous genus Fuckelia of the Melogrammeae. Placosphaeria, on the other hand, has an effused stroma resembling Rhytisma, or certain species of Phyllachora. The four remaining genera possess a stroma, more or less like Valsa, especially so in Cytospora, in which the sporules are small and sausage-shaped. It is probable that all the species in this genus are stylosporous conditions of Valsa. The genus Cytosporella only differs from Cytospora in having the sporules either globose or ovoid; and Fusicoccum again in the sporules being large and straight, and mostly fusiform; so that these three genera resemble Valsa in habit, but differ amongst themselves in the form of the sporules. Centhospora might be included in the same series, but the stroma is firmer, and the spore-bearing cells have the converging necks mostly united in a central orifice. The sporules are cylindrical and typically straight. It is very usual, even if not universal, for the mature sporules which are held together in a pasty mass to be ejected in the form of a tendril, or a contorted thread. Thus concludes the section Hyalosporae of the Sphaerioid family of the Sphaeropsideae, including an enumeration of not less than 2625 species.

The Phaeosporae section has the sporules continuous, and coloured either brown or sooty. The number of genera is comparatively small, and of these four have the perithecia subglobose and smooth. Two of these are practically old genera, since Sphaeropsis was recognised by Fries, although not limited, as now, to species with coloured sporules. It is in all respects the corresponding genus to Diplodia, but with continuous, and not uniseptate, sporules, as in that instance. Coniothyrium is closely allied to Sphaeropsis, but the perithecia are normally smaller, as are also the sporules, which are large and elliptical in Sphaeropsis, small and globose, or ovoid, in Coniothyrium. The genus Harknessia closely resembles Melanconium in the sporules, and also in their ejection when mature, and the consequent blackening of the matrix, but differs in the possession of a distinct perithecium. In

Hypocenia the sporules are fusoid and pale brown. Levieuxia is a South African genus, containing a single species, with a stipitate perithecium, which is fissured at the apex when mature. The only genus with hairy perithecia is Chaetomella, which is the analogue of Chaetomium, but deficient in asci. The residue of the section consists of genera in which the perithecia are compound or caespitose. Haplosporella is, in fact, a caespitose Sphaeropsis, the perithecia being aggregated in dense erumpent pustules, resembling those of some species of Botryosphaeria. Weinmannodora has a stroma which is hemispherical and carbonaceous, with radiating fertile cells, containing globose dark sporules. Cytoplea consists of a single species, in which the stroma is at first pulvinate, then confluent and effused. Practically the entire section is represented in Europe by Sphaeropsis and Coniothyrium, with smooth perithecia; and Chaetomella, with setose perithecia; and in the compound genera by Haplosporella.

The *Phaeodidymae* is also a small section, with uniseptate coloured sporules, and is, in fact, entirely made up of species which entered into the old genus *Diplodia*, as recognised by Fries. Thus *Diplodia*, as limited, contains species with a smooth perithecium, and coloured sporules, not having a mucous envelope; *Macrodiplodia*, with similar smooth perithecia, but coloured sporules having a mucous envelope, as in the sporidia of *Massaria*; *Chaetodiplodia*, with hairy perithecia, and sporules as in *Diplodia*. The remaining genus with simple perithecia is *Diplodiella*, in which the perithecia are almost superficial, and flourish on decaying wood. The single composite genus is *Botryodiplodia*, with the perithecia densely aggregated in erumpent pustules as in *Haplosporella*.

The section Hyalodidymae is characterised by hyaline uniseptate sporules. Two genera correspond to Phyllosticta in Hyalosporae, in that the species are mostly parasitic on living leaves, collected on discoloured spots. In Ascochyta the sporules are simply uniseptate, but in Robillarda the sporules are uniseptate and crested at the apex with long setae, resembling in this respect the genus Pestalozzia. In three other genera the smooth perithecia are scattered and not seated on discoloured spots. Actinonema has the perithecia seated upon a radiating

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE 265

adnate subiculum as in *Asteroma*, but with different sporules. *Darluca* has no subiculum, but the perithecia are parasitic on old Uredines, and in *Diplodina* the species grow on branches the perithecia, and even the sporules, resembling *Diplodia*, save that they are uncoloured. In *Cystotricha* the perithecia dehisce as in *Hysterium*, with a gaping fissure, and the sporophores are septate and constricted, so as to possess a moniliform appearance. In the only remaining genus, *Rhynchophoma*, the perithecia resemble *Phoma* externally, except that they are rostellate and the sporules are uniseptate.

The succeeding section, Phragmosporae, has the sporules multiseptate, and is represented in two divisions, in one of which the sporules are brown, and in the other hyaline. The former is the most numerous in genera and species. The old genus Hendersonia, as interpreted by Berkeley, has been divided, and is now restricted to such species as possess coloured sporules. The perithecia are papillate, covered by the cuticle. In Couturea the species have superficial perithecia, which are seated on a stellate subiculum, somewhat after the manner of Asteroma. In the two small genera Angiopoma and Lichenopsis the perithecia dehisce by an operculum at the apex. In the former the perithecia are superficial and hairy; in the latter immersed and smooth. Cryptostictis somewhat resembles *Pestalozzia* in the septate sporules being furnished at both extremities with a hyaline bristle, whereas in Pestalozzia the cilia are more than one, and confined to the apex of the sporule. In another small genus, that of Prosthemium, the sporules are also peculiar, in being joined together at the base in a stellate manner (Fig. 122). The compound species are confined to a single genus, in which the perithecia are immersed in a stroma, as in Dothideaceae. This genus is Hendersonula, and is, in fact, a compound Hendersonia.

The Hyalophragmiae, in which the sporules are colourless, includes but two genera: Stagonospora, which is practically Hendersonia with hyaline sporules; and Mastomyces, in which the perithecia are elongated and superficial, resembling scattered perithecia of the rather obscure genus Corynelia, which is ascigerous.

The Dictyosporae, in which the sporules are coloured and

muriform, consist almost absolutely of one type, that of *Camarosporium*, which resembles *Hendersonia* in habit and appearance, growing upon branches, covered by the cuticle. *Cytosporium* only differs in the perithecia being subsuperficial, growing on naked wood. *Dichomera*, in which the perithecia are immersed in a stroma, as in *Dothideaceae*, is consequently compound. The doubtful genus *Endobotrya*, contains but one species, which is North American.

A rather important section is the Scolecosporae, in which



FIG. 122.—Prosthemium section with sporules.

the sporules are very much elongated, so as to be thread-like, or rod-like, and either hyaline or faintly coloured. The principal genus is *Septoria*, of which the species are in greater part parasitic, growing on living leaves or the green parts of plants. The minute perithecia are flattened and innate, and typically aggregated upon discoloured spots. This genus is analogous to *Phyllosticta*,

from which the species cannot be distinguished except There is a suggestion of genetic conby the sporules. nection between some of the species and the ascigerous genus Sphaerella, but this has not been demonstrated. Phlaeospora includes such species as would otherwise find a place in Septoria, were not the sporules thickened, and comparatively shorter. Rhabdospora scarcely differs from Septoria except that the perithecia are not seated on discoloured spots, and are confined to twigs and the stems of herbaceous plants. It bears about the same relation to Septoria that Phoma does to Phyllosticta. Phlyctaena would otherwise be the same as Rhabdospora, only that the perithecia split with a fissure, and become deficient above. In the small genus Gelatinosporium, the perithecia dehisce broadly and irregularly, the sporules in the interior forming a gelatinous mass. There are two genera in which the perithecia are distinctly rostrate as in Sphaeronema, from which genus the species have been separated, on account of the difference in the sporules : Sphaerographium, in which the sporules are continuous; and Cornularia, in which they are septate. Of the three compound genera, Eriospora

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE 267

has the stroma small and depressed, with the sporules connected in bundles of four; *Dilophospora* has a crustaceous stroma, with the sporules crested with cilia at each end; whilst *Cytosporina* accords with *Cytospora* in general features, but the sporules are thread-like and curved, or flexuous. Possibly few of the species are autonomous. There remain but two aberrant genera to be alluded to, and these are *Micula* and *Micropera*. The species occur on bark and often resemble lenticels, or are clustered like species of *Cenangium*, of which they are said to be the pycnidia; the sporules are elongated and nucleate.

The second family, Nectrioideae, bears the same relation to the Sphaerioideae as the Hypocreaceae to Sphaeriaceae in the Pyrenomyceteae. The perithecia and the stroma, when present, are fleshy or waxy, and pale or bright coloured. The arrangement here is the same as in the preceding family, primarily based on the sporules, so that the sections correspond. The first section is the Hyalosporae, in which the sporules are continuous and hvaline. Most of the genera are simple, and only one is composite. Of the four in which the perithecia are not beaked, only one needs particular reference, as the residue contain only a single species. Zythia resembles a scattered Nectria in appearance, with ovoid or oblong sporules. Sphaeronemella is analogous to Sphaeronema, and has the perithecia rostrate. The only composite genus is Aschersonia, of which the species might be mistaken at first for species of Hypocrea, the structure and habit being that of Hypocrea without asci. In the only species of the genus Dichlaena the perithecia have a double tunic, and the sporules are minute and globose. In Didymosporae the only genus is Pseudodiplodia, which corresponds to *Diplodia* in the brown uniseptate sporules, but differs in the colour and texture of the perithecia. In Phragmosporae all are hyaline. Stagonopsis corresponds to Stagonospora, with like sporules; but in Chiastospora the sporules are arranged in four rays. Only one species is known in each genus. The Scolecosporae has but one genus, with filiform sporules. This is Polystigmina, a stylosporous form of the ascigerous genus Polystigma, in which the perithecia are immersed in a discoid stroma. A small group, consisting of

three genera and three species, has been placed in proximity to the *Nectrioideae*, although not quite conforming thereto, on account of their approach to a cup-shaped receptacle, so that their position can only be regarded as provisional. *Hysteromyxa* combines the habit of a *Hysterium* with the fruit of a Myxomycete. *Patellina* with the habit of a *Patellaria* has stylosporous fruit. And *Cyphina* has the appearance of an *Excipula*, but is bright coloured and garnished with white hairs, so as to offer an analogy to *Volutella*. All of these require fuller investigation, and none are European.

The family Leptostromaceae diverges from the previous families in losing much of the Sphaeria-like habit, and approaching that of some of the Hysteriaceae, with occasional suggestions of Phacidiaceae. The perithecia are more or less distinctly dimidiate, or scutiform, with or without an ostiolum, or fissured longitudinally, either membranaceous or carbonaceous, black, and either erumpent or superficial. Under the carpological arrangement, the Hyalosporae are again the most numerous, and resolve themselves into two subdivisions, in one of which, although the perithecia are destitute of a definite mouth, they dehisce in diverse ways, but not with a longitudinal fissure. In the other subdivision the perithecia split longitudinally after the manner of the Hysteriaceae. Leptothy-



FIG. 123.—Leptothyrium.

rium is the chief genus in the first subdivision, with a dimidiate and shield-like perithecium, which does not split by a longitudinal fissure, but soon cracks all round and falls away (Fig. 123). Some of the species are believed to be the stylospores of certain species of *Coccomyces*. The genus *Piggotia* has an irregular depressed perithecium which does not fall away. *Melasmia* is allied, but in this genus the perithecia are innate in a

black effused stroma, growing on fading leaves. The species are the stylosporous condition of *Rhytisma*, which develop asci in the same stroma after the leaves have fallen and rested on the ground during winter. *Actinothecium* has an orbicular scutate perithecium, which dehisces by several radiating fissures. In the other group, in which the perithecia split longitudinally—the chief is *Leptostroma*, which corre-

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE 269

sponds to Leptothyrium — the perithecia are elongated and fissured after the manner of Hysterium, and some of them are probably the stylosporous condition of species of Hypoderma or of Lophodermium. Labrella has nearly circular perithecia, which are innate, and sometimes formed from the changed matrix, dehiscing by a longitudinal crack. A final genus, Sacidium, differs from all the rest in the perithecia not being distinctly parenchymatous. The sporules are often globose. The Phaeosporae, with coloured continuous sporules, consist of but one small genus, with scutate perithecia pierced in the Of this single genus, Pirostoma, only one species is centre. The Phragmosporae have all hyaline sporules, which known. in Discosia are fusoid and ciliate at each end. In Entomosporium the sporules are two-celled, with a lateral smaller cell on each side at the septum, so as to be cruciate, each with a This is the same genus as is sometimes known under cilium. the name of Morthiera. The Scolecosporae, with long filiform sporules, include the genus Actinothyrium, which has flat shield-like perithecia, delicately fringed all around the margin; and Melophia, in which the similar perithecia are corrugated, but not fringed at the margin. Leptostromella consists of species of Leptostroma, as originally interpreted, which have long filiform sporules. In other respects with the habit and appearance of Leptostroma. The Leptostromaceae are most common on leaves, or the stems of herbaceous plants, but with only a few exceptions appear to be saprophytic.

The last family is the *Excipulaceae*, in which there is a nearer approach to cupulate forms. In its general character the perithecium, or receptacle, is cup-shaped, patellate, discoid, or hysteriform, in all of which it is at first nearly spherical, but soon open; and either smooth or hairy, commonly erumpent, and then superficial, so as almost to resemble minute black *Pezizae*, with which some of the species were formerly associated. The *Hyalosporae* are again the largest section, and may be divided into those which have the receptacle smooth and those in which the receptable is hairy or bristly. The smooth cupped are of two kinds, namely, those in which the receptacle is cupshaped and those in which the receptacle is split longitudinally, or is valvate. The cup-shaped, smooth-surfaced group contains

Godroniella, a genus in which the receptacle is composed of agglutinated hyphae, in other respects scarcely differing from the next genus, Excipula, in which the excipulum is cellular, membranaceous, or tough, and black. The genus Excipula of Fries, and many subsequent authors, was rather a heterogeneous one, even including some ascigerous species, and the residue are now distributed over six different genera. Heteropatella differs in the perithecia being thicker and more leathery, with the mouth always contracted and torn, the sporules fusiform, growing upon branched sporophores. In Dothichiza the black receptacles are mostly erumpent, often gregarious, at first closed, then rather cup-shaped, and are often the spermogonia of species of Cenangium. Sporules oblong and continuous. In Lemalis the receptacles are membranaceous, or rather fleshy, coloured, but not black. Catinula has the receptacles tough or horny, and black, rather cup-shaped, disc often bright coloured. Discula corresponds to Discella, but the sporules are continuous. The receptacles are discoid or patellate, often imperfect, black or coloured. Hereafter follow the genera in which the perithecia are hysteriform or valvate. In Sporonema the receptacles are valvate, dehiscing with angular teeth, as in Phacidium, of which they are possibly a stylosporous condition. Pleococcum is scarcely distinct from Sporonema, although the contents are assumed to be more mucilaginous. Psilospora closely resembles Dichaena, of which it is evidently a stylosporous state. The perithecia dehisce in the manner of Hysterium, with two lips, and occur upon living bark of trees. The remaining genera of the Hyalosporae possess hairy perithecia. The genus Amerosporium has the receptacles cup-shaped, and corresponds to Excipula; but the cups are setulose, the sporules are naked at the ends. In Dinemasporium the habit and external appearance are the same, but the sporules have a hyaline bristle, or awn, at each end (Fig. 124). Polynema differs in having the apex of the sporules crowned with about four awns. In the next section, the Hyalodidymae, there are but two genera. In Discella the perithecia are normally discoid, sometimes imperfect, or formed from the matrix, a long time covered by Sporules oblong, uniseptate, and hyaline. the cuticle. In Pseudopatella the receptacle is cup-shaped, almost superficial

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE 271

tough and black, with a pallid disc. Possibly a stylosporous form of *Durella compressa* is the only recorded species. The section *Phragmosporae* contains two genera which are offsets from the old genus *Excipula*. These are *Excipulina*, with

smooth receptacles and multiseptate sporules; and *Excipularia*, with setose receptacles and multiseptate sporules. In the remaining genus, *Pilidium*, the receptacles are erumpent, discoid, and membranaceous, blackish and torn at the margin, with a pallid disc. The section *Scolecosporae* alone remains, containing three genera in which no definite stroma is present: *Schizothyrella*, with the perithecia hemispherical, then torn at the margin, the filiform sporules breaking up into cylindrical joints; *Protostegia*, in which the

receptacles are discoid, at first covered, then



FIG. 124. — Sporules of Dinemasporium.

exposed, margin torn or fringed, disc gelatinous, sporules thread-like, but not breaking up; and Oncospora, with discoid or cup-shaped receptacles, usually gregarious, erumpent, disc gelatinous and the sporules clavate, hamate (curved like a sickle) or sigmoid (like the letter S). The only compound genus is *Ephelis*, in which an effused, sclerotium-like black stroma bears the cup-shaped receptacles, with filiform sporules. It is analogous to a genus of *Discomyceteae*, to which the name of *Ephelina* has been given.

This running commentary on the *Sphaeropsideae* has made it manifest that at many points the genera, or some species, have a close relationship with some of the *Ascomyceteae*; but even if all these were removed, there would still remain an imposing array of species against the autonomy of which no word of calumny has yet been offered. The *Sphaeropsideae* may not be so attractive or interesting as the *Pyrenomyceteae*, but they equally claim recognition, until the alleged dimorphism can be proved against them.

The *Melanconieae* have undoubtedly a close affinity with the *Sphaeropsideae*, with which they have always been associated. The chief distinction, and the only one which can be insisted upon, is that the perithecia—so universal, under some form, in the *Sphaeropsideae*—are absent in the *Melanconieae*. The habit
is nearly the same, except that the pustules are always erumpent, and never superficial, and the sporules are similar in form and size, produced similarly at the apex of short sporophores. The difference therefore is reduced to that of the character of the walls of the cavities in which the sporules are engendered. In the Melanconieae there are definite cavities, beneath the cuticle, which correspond in function to immersed perithecia; yet these cells have no heterogeneous walls, but are simply modifications of the matrix. In many cases they are distinctly modified so as to appear as pseudoperithecia; in some there is merely a compact base, formed by the mycelium into a sporebed, upon which the sporules are developed, and when mature are ejected, in a more or less gelatinous mass, through fissures or orifices in the covering cuticle. The spore-bodies are termed conidia by Saccardo, as they are in the Hyphomyceteae, but we prefer to employ the same term as that adopted in the allied Sphaeropsideae, and distinguish them as sporules.

The technical definition of the *Melanconieae* is to the effect that they are Fungi without perithecia or asci, forming subcuticular pustules, which are partially erumpent, discharging the sporules through openings in the cuticle, such sporules being produced on a proligerous stratum, growing upon distinct or obsolete sporophores, and either in themselves continuous or septate, either hyaline or coloured.

The arrangement adopted is similar to that of the Sphaeropsideae, the primary sections having relation to the character of the sporules. The Hyalosporae include those which have oblong, or shortly cylindrical continuous hyaline sporules, whether solitary on the sporophores or produced in chains. Four genera are indicated in which the sporules are solitary on the sporophores, two being found mostly growing on leaves, and two upon branches. The distinctions between Hainesia and Gloeosporium, which are the two genera that flourish for the most part on living leaves or succulent fruits, are scarcely sufficient, since they resolve themselves into this, that in Hainesia the pustules are brightly coloured, and in Gloeosporium gray, pallid, or dull coloured. Hence we can treat them both as a single genus. These parasites are amongst the most destructive with which the horticulturist

IMPERFECT CAPSULAR FUNGI-SPHAEROPSIDEAE 273

has to contend, or, at the least, the most insidious, and least subject to control. They do not spread over such tracts as the potato disease and the hop mildew, but the infected plants upon which they appear are doomed, and these often the rarest and most valuable. The first external indication is usually in the form of small elevations of the cuticle, or little warts, which cover the concealed pustules; for a long time these remain unbroken, but when the sporules are mature the cuticle is ruptured, and a globule, or tendril, of agglutinated sporules emerge through the orifice. These sporules are either elliptical or elongated, usually much longer than broad, and often of considerable size, but without septum or colour. Including the two supposed genera, not less than some 230 species are known, to say nothing of Marsonia, which is a corresponding genus with uniseptate sporules, and similar habit and propensities. The two corticolous genera Myxosporium and Melanostroma are not clearly distinct from each other. The habit is similar to Gloeosporium, but the species are found chiefly on dead bark, and therefore not parasitic, or destructive. Many of the species are credited with being stylosporous conditions of various ascigerous Fungi. The sporules resemble those of Gloeosporium. The series of genera in which the sporules are produced in chains is represented by only a few species. Hypodermium has black pustules, which, being elongated, resemble the perithecia in Hypoderma, a genus of the Hysteri-Myxosporella is simply Myxosporium with the sporules aceae. catenulate. Blennoria has discoid pustules, which bear a resemblance to Puccinia, to which Agyriella is closely allied; but the pustules are at first gelatinous, becoming hard and shining. In Trullula the pustules are compact and erumpent, often having the appearance of perithecia; the sporules are sometimes coloured. In the two genera Myxormia and Bloxamia the pustules are apparently pezizoid; that is to say, the form resembles a shallow cup, or concave disc, without a receptacle. In Myxormia the sporules are joined in a chain, by a narrow isthmus; and in Bloxamia they are truncate, and closely applied to each other. There are two other genera, Colletotrichum, which is simply a Gloeosporium, with the margin of the pustules hairy; and Pestalozziella, in which the sporules are

cristate, and therefore analogous to Robillarda but with continuous sporules, or a dwarfed form of Pestalozzia without colour and without divisions. The next section is a modified one, or at least the Scoleco-allantosporae combines Scolecosporae and Allantosporae in a single section. In one genus, that of Cylindrosporium, the sporules are really filiform; in Cryptosporium and Libertella elongated and falcate, but scarcely filiform; and in Nemaspora they are allantoid, or sausage-shaped. In Cylindrosporium the species are parasitic on living leaves, and thus correspond to Gloeosporium. In the other three genera they are saprophytic, chiefly affecting the bark of dead branches. In Cryptosporium the sporules are mostly rather large and robust, but in Libertella slender, oozing out in brightly coloured tendrils. Nemaspora somewhat resembles Libertella, but the sporules are shorter, and allantoid. In all three genera there are many species which are regarded as stylosporous forms of ascigerous Fungi, and suggest analogy to Cytospora in the Sphaeropsoideae.

The section *Phaeosporae* is the most typical, and includes the genus *Melanconium*, which is almost the same as Fries left it, with subglobose or oblong dark-coloured sporules, often oozing out and blackening the orifice of the pustules. Some of the species are associated with *Sphaeriaceae* of the genus *Melanconis*, but others may prove to be autonomous. *Cryptomela* is analogous to *Cryptosporium*, but with coloured sporules. *Thyrsidium* is, however, a genus by itself, in which the contents of the pustules are gelatinous, and the sporules are minute, but clustered in chains at the apex of elongated sporophores, in a capitate manner, involved in a mucous envelope.

The *Didymosporae* include four genera, in which the sporules are uniseptate, and in two of them coloured, whilst in other two they are hyaline. Of the former, *Didymosporium* corresponds to *Melanconium*, but with two-celled sporules; and *Bullaria*, with a single species, has the conidia connected in chains by a narrow hyaline isthmus. Of the two genera with hyaline sporules, it has already been intimated that *Marsonia* is the analogue of *Gloeosporium*, with the same habit and the same parasitic character, but the sporules are septate. Septo-

myxa, in like manner, corresponds to Myxosporium, growing on dead branches, but with uniseptate sporules.

The section Phragmosporae includes such species as have sporules with two or more septa, whether hyaline or coloured; and thus we have two subsections, the Phaoeophragmiae and In the former Stilbospora is the anathe Hyalophragmiae. logue of Melanconium and Didymosporium, with sporules soon oozing out and blackening the orifice; whilst Coryneum forms compact pustules, in which the sporules are for a long time attached to their pedicels, and do not ooze out and blacken the matrix. In habit the species are more pulvinate and erumpent, being held together almost as compactly as if enclosed in a Scolecosporium resembles Coryneum, but the perithecium. sporules are beaked at the apex. Asterosporium has more the habit of Stilbospora, but the sporules are compound, or rather triradiate, resembling three sporules of Stilbospora grown together at the base and diverging above in three rays on the same plane. In another genus, Seiridium, the septate brown sporules are united to each other by a hyaline isthmus, so as to form a chain. The two remaining genera, having ciliate

sporules, are *Hyaloceras*, in which the multiseptate brown sporules have a single curved awn at each extremity; and *Pestalozzia*, in which the sporules are crested by one or more hyaline cilia, which are usually divergent when more than one, and the central cells of the sporules are commonly coloured (Fig. 125). The *Hyalophragmiae* includes but three genera; that of *Rhopalidium*, with one little-known species, has clavate, multiseptate, hyaline



FIG. 125.—Sporules of Pestalozzia.

sporules, aggregated in little innate brown pustules on the leaves of plants; and *Septoglaeum*, which is practically *Gloeosporium*, or *Marsonia*, with more than one septum to the sporules. The remaining genus is *Prosthemiella*, which is the analogue of *Prosthemium*, but without a perithecium, and the stellate sporules are hyaline. It will facilitate determination to remember the instances, which are so constantly recurring, in which Fungi possessing the same habit

and external appearance find their place in sections widely removed from each other, as the consequence of the septation, or multiseptation, of the sporules. Thus we have, for instance, *Gloeosporium* with continuous sporules in *Hyalosporae*; with filiform sporules, as *Cylindrosporium*, under *Scoleco - allantosporae*; with uniseptate sporules, as *Marsonia*, under the *Didymosporae*; and with multiseptate sporules, as *Septoglaeum*, under *Hyalophragmiae*.

There remains but one small section to notice, and that is the *Dictyosporae*, in which the sporules are divided in both directions, so as to be muriform. Of the two genera, *Steganosporium* is the analogue of *Coryneum*, having compact pulvinate pustules, but with muriform, coloured sporules; and *Phragmotrichum*, in which the sporules are concatenate, or in chains, as in *Myxormia* and *Seiridium*, and is practically *Seiridium* with the sporules septate in both directions.

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CHAPTER XXIII

MOULDS-HYPHOMYCETES

In their internal relations to each other, and their external relations to the remaining orders, the Hyphomycetes are undoubtedly a well-defined and natural group. It may be, and probably is, too rash an assumption to contend that all the species are form-species, and only represent the conidial stage of more perfect Fungi; nevertheless a large number of them have been demonstrated to be merely transitionary, although the precise mode of continuity has not been made clear. In such a case the only reasonable course to adopt is to recognise their morphological distinctions, and treat them, for all purposes of classification, on the supposition that they may be autonomous, and leave to the future, when their life-histories are thoroughly known, to develop their true affinities and relationships. The number of described species falls but little short of 5000, and such a number is too large and important to remain unrecognised, or without definite classification, within the limits of present knowledge. Because many of the species of Isaria have been ascertained to represent the conidia of Cordyceps; because certain of the subgenus Polyactis may be the conidia of Sclerotinia; or even the entire genus Zygodesmium may be so intimately related to resupinate Thelephorae that definite limit cannot be assigned between them, it would be folly to expunge the whole upon suspicion, and thus increase the difficulties in the way of the student in the pursuit of knowledge along a path already sufficiently thorny and stony.

The general characteristics of the order are, that the spores, or conidia, are naked or free, as they are in no other order, except the *Hymenomycetes* and some of the *Phycomycetes*;

whilst they differ from the former in having no hymenium and being deficient in true basidia, and from the latter in the absence of sexual reproduction. The Fungi themselves are either superficial or subsuperficial, and the hyphae or conidiabearers are, for the most part, strongly developed. Typically there is a creeping, septate mycelium, seated upon or penetrating the matrix, which gives rise to erect, more or less developed, hyphae, or spore-bearers, which produce terminally or laterally naked spores or conidia. Most of them are saprophytic on dead animal or vegetable substances, whilst a limited number are parasitic upon living plants.

The four families are the Mucedineae, or "white moulds," with the threads colourless, pale, or brightly coloured, often fasciculate, but not coherent, with conidia of the same colour : the Dematicae, or "black moulds," having the hyphae brown, or black, rather rigid, and not coherent, rarely pale and then with the conidia blackish; the Stilbeae, with the hyphae either pallid or brown, densely cohering in long stem-like fascicles: and the *Tubercularieae*, with the hyphae pallid or brown, densely conglutinate in wart-like pustules, or sporodochia or spore-beds, often forming a rather thick stroma at the base. Thus, it will be observed that in two of the families the hyphae are free and distinct from each other, being typically pale in the one and dark coloured in the other; whilst in the other two families the hyphae are closely coherent and elongated in the one, and shortened, conglutinate, and stromatic in the other. The latter are for the most part erumpent and pustular.

This, then, is the primary division of the *Hyphomycetes*, of which the largest, and most typical, of the two great sections is that in which the erect threads or conidiophores are free of each other, and not united in a common stem. These are the moulds, which as yet are not known to possess any but a simple and asexual reproduction, by means of conidia, but which are considered to be genetically connected, by some means not clearly manifest, with species belonging to other orders of Fungi, and especially of the *Ascomycetes*. For the better understanding of the principles on which the classification of these imperfect Fungi has been reduced to a system, we must examine the sections in further detail, commencing with

MOULDS-HYPHOMYCETES

the *Mucedines*. In this family, as in all the primary divisions of the orders devised by Saccardo, the spores, or conidia, hold the first place, so that not only are the genera limited by the septation, or non-septation, of the spores, but this also forms the basis of the first subdivision into the *Amerosporae* (Fig. 126), in which the conidia are spheroid or shortly cylindrical;

the *Didymosporae*, in which the conidia are oblong or fusoid, and uniseptate; the *Phragmosporae*, in which the more elongated conidia are two, three, or many septate; the *Staurosporae*, in which the conidia are stellate, radiate, or trifurcate; and the *Helicosporae*, in which the elongated conidia are spirally convolute. It is not clear that the last is a necessary or homogeneous section, or that it is at best any other than a subsection of the *Phragmosporae*, with the elongated and septate conidia, instead of being simply curved or flexuous, curved more strongly so as to be spirally convolute. Thus, then, having discovered that any given mould



FIG. 126. — Menispora lucida, one of the Amerosporae.

has a simple or compound stem, it is incumbent to ascertain, on the assumption that the stem is simple, whether the threads are carbonised, or only hyaline, or bright coloured, and thus discover the one of the four families in which its place has to be found. It being determined, for example, that the mould in question is a Mucedine, the next step is to find the conidia, and ascertain if they are continuous, or in what manner they are septate. Up to this point it may be possible to place a sterile mould, but from this point forwards it is manifestly impossible to proceed, in the absence of all fructification. This leads us to observe how utterly futile it is to attempt the determination of even the genus, much less the species, of any mould, in the absence of conidia. Novices are apt to infer that it is not only possible, but easy, to give a name to any mouldy tuft which presents itself as such to the naked eye, but possessing only mycelium and threads, without any indication of the character of the spore. The labour which is expended in any such endeavour is wasted, and it is always better to abandon the task at once, not only in this but in other orders, unless

conidia, or spores, of some kind can be detected, otherwise the endeavour can only terminate in vexation of spirit.

Resuming our survey of the system at the point where it is necessary to determine the character of the spore, or conidium,



FIG. 127.-Rhopalothe Macronemeae.

and if it is uniseptate to seek it in the Didymosporae, but if further septate in the Phragmosporae, we shall soon discover that the greater number of species have conidia which are not septate at all, and therefore belong to the section Amerosporae. At this point we may leave the conidia and revert to the hyphae or threads which bear them. In some cases we shall observe that the conidiophores, myces representing or conidia-bearers, are long threads, which are sometimes simple, but in most cases branched once, twice, or many times; these generally form

large, conspicuous woolly tufts, easily recognised by the naked eye, and constitute the subsection Macronemeae, or, as we might say, the subsection in which the threads or hyphae are strongly developed, and quite distinct from the conidia (Fig. 127). Then there is another and smaller section, the Micronemeae, in which

the threads are very short, and mostly unbranched, so short, indeed, as only just to be recognised, and, at times, scarcely different from the spores or conidia themselves (Fig. 128). In nearly all the subdivisions of the various families of the Hyphomycetes, such subdivisions being based upon the character of the conidia, the genera are associated in these two groups of



FIG. 128.—One of the Micronemeae Aegerita.

Macronemeae or Micronemeae, according as the conidia-bearing threads are long and well developed or short and almost It would be wearisome and unnecessary here to obsolete. detail all the varied modifications of the conidia-bearers, or the conidia, which are taken advantage of in the construction of genera, or groups of genera. It must suffice to say that most of the distinctions are based upon the form, or mode of arrangement, of the conidia about the threads. For instance,

MOULDS-HYPHOMYCETES

a distinction is made between such conidia as are solitary and those which are produced in chains, or catenulate (Fig. 129); between those which are solitary and those which are clustered

at the apex of the hyphae, or its branches, so as to form more or less dense heads, or clusters of conidia; between those in which the conidia are terminal and those in which they are lateral or dispersed. Other distinctions are derived from the hyphae themselves, whether simple or branched; or if simple, whether inflated at the apex or not; and if branched, whether simply furcate, repeatedly divided, or if the branches are arranged in whorls or verticillate. All these are details which are readily gathered from the diagnoses of the separate genera, and we have said sufficient to indicate the principal features which have to be taken



FIG. 129.—*Penicillium* with the conidia in chains.

into account in the determination of the genus to which any particular mould may belong.

Although the above observations apply in the first instance to the Mucedines, they apply also generally to the Dematieae, with the exception that in the divisions based on the forms of the spores, or conidia, there will be found an additional division, the Dictyosporae, in which the conidia are divided in both directions, so as to be clathrate or muriform. Some of these conidia will therefore present the appearance of twenty or more simple cells, aggregated into one large complex conidium. Judging from the facility with which each cell of these compound conidia germinates, it may be inferred that each cell is a reproductive unit, and is in itself a perfect conidium, capable of reproducing the species. So in respect to uniseptate or multiseptate conidia, in a linear series, each cell is capable of germination, and even, in some instances, of separating itself from its sister cells, when arrived at maturity (Fig. 130). Mr. Worthington Smith, in his observations on Fusarium solani, has intimated that, although some of the segments of the conidia germinate at once, others are capable of undergoing a period of rest. He says, "Sometimes these little

bodies do not germinate at once, but hibernate for a short time, generally varying from three weeks to three months, commonly two months, and during this period they become slightly spinulose and faintly tinted with a brownish hue. These



FIG. 130.—Conidia of *Fusarium*. B, mature conidium; C, cells germinating; D, cells separating, and becoming rounded; E, separated cell after a period of rest-germinating. After Smith. Macmillan and Co.

little bodies, therefore, hibernate after the manner of resting spores, and it is possible that many of them rest during the entire winter." 1 Assuming that the segments of the conidia of Fusarium are capable of forming a thicker integument, and hibernating through the winter, there is no reason why, from analogy, other

conidia, belonging to other genera, may not be capable of a like modification, and thus aid in the perpetuation of the It is almost certain that the thin-walled conidia species. are unable to survive the winter, and hence the question arises as to how the rejuvenescence of the Hyphomycetes is assured; for, although in some cases a perennial mycelium may explain the difficulty, it cannot do so in the parasitic species, such as Ramularia, Ovularia, and Cercospora, where the destructive fungus appears as a pest on the living leaves, year after year. As an example, the leaves of the "ground ivy" (Glechoma) through the autumn will present hundreds of leaves with the white blotches of Ramularia calcea, sometimes every leaf more or less affected, and during the winter most of these leaves will die and decay. With the spring there will be a carpet of green leaves again, without a spot of Ramularia; but as summer advances the pest appears as profusely as ever, and the

¹ Diseases of Field and Garden Crops, by W. G. Smith, London (1884), p. 33.

MOULDS-HYPHOMYCETES

leaves are blotched with white. Can we answer the question satisfactorily and confidently as to how the continuance of the parasite has been secured? It is possible that a perennial mycelium within such of the plant's tissues as have survived the winter may be a sufficient cause, but it is doubtful whether this is the only method in which the perpetuation of the *Ramularia* has been assured. If it should be contended that the decaying leaves and petioles of the previous year must contain the germs of the parasite, and that the young leaves are infected thereby, this only removes the difficulty a step further, for it has to be shown in what form the germs have been preserved, as it must have been by some form of resting spores or a resting mycelium capable of producing germinating bodies. This is one of the problems which is left for the future to solve.

So many of the Mucedines and "black moulds" have been ascertained to have relationships with the higher Fungi that it is impossible to do more than briefly allude to a few. In the genus Oidium a number of the species are the conidia of species of the Erysiphei, such as Oidium leucoconium, the rose mildew, of Sphaerotheca pannosa; Oidium erysiphoides of Erysiphe Martii; Oidium monilioides of Erysiphe graminis. The common fruit mould Aspergillus glaucus has the reputation of being the conidia of Eurotium herbariorum. Some of the species Botrytis, of the subgenus Polyactis, are the conidia of small species of *Peziza*, such as *Sclerotinia sclerotiorum*. The bright yellow mould Sepedonium chrysospermum, which attacks decaying *Boleti*, and converts them into a mass of golden powder, develops Hypomyces chrysospermum, one of the Sphaeriaceae, of which the mould constitutes the conidia. If we investigate the British species of this genus Hypomyces,¹ we shall find that all have their conidia in some of the moulds. As, for instance, Verticillium agaricinum of Hypomyces and Verticillium lactescentium of ochraceus, Hypomyces terrestris; also Verticillium microspermum of Hypomyces broomeanum; Diplocladium penicilloides of Hypomyces aurantius; Diplosporium album of Hypomyces violaceus, etc. The same kind of association prevails also amongst the

¹ Monograph of British Hypomyces, by C. B. Plowright.

283

Dematieae, for Trichosporium fuscum is found forming the subiculum of Rosellinia aquila, and the common Bispora monilioides is reputed to constitute the conidia of a small Peziza, hence called Bisporella monilifera; but this appears to us a doubtful case. Fusicladium depressum is reported to be the conidia of Phyllachora angelicae, and Polythrincium trifolii of Phyllachora trifolii. Species of Cladosporium, of Cladotrichum, and Helminthosporium respectively are believed to be related genetically to various species of the Sphaeriacei, and especially species of Macrosporium to certain species of Pleospora. It is sufficient for our purpose to suggest these relationships as indicating the evidence on which the Hyphomycetes are concluded to be imperfect Fungi, and principally conidial forms of Ascomycetes.

After this digression we may return to the two inferior



FIG. 131. - Stilbum vulgare.

families of the order, in which the hyphae are fused into a common stem. The *Stilbeae* (Fig. 131) are of a more imposing appearance than the *Tubercularieae*, and perhaps of a higher development. There are not more than about five hundred described species, and these are

grouped in two parallel sections: the *Hyalostilbeae*, in which the hyphae and conidia are pallid; and the *Phaeostilbeae*, in which the hyphae and conidia are typically dusky coloured. Thus these two sections correspond to the *Mucedineae* and the *Dematieae*.

The Hyalostilbeae, as far as at present known, are less variable in fructification than the Phaeostilbeae, it being found necessary to recognise but two of the subsections: the Amerosporae, in which the conidia are globose or oblong, and continuous; and the Phragmosporae, in which the conidia are septate. The latter is a very small section, of some seven or eight species, so that practically the Hyalostilbeae have small and continuous spores, or conidia. The subsidiary arrangement is very much on the same lines as in the moulds. The principal genera are the old ones of Stilbum and Isaria, with

MOULDS-HYPHOMYCETES

The former has a capitate form, typically a comtheir allies. pound stem, with a globose head; and the latter assumes a cylindrical or club-shaped form, the stem and head being The surface is generally powdery with the continuous. minute conidia. As to their autonomy, it is known that, in several instances, the species of Stilbum represent the conidia of a peculiar genus of the Sphaeriaceae, that of Sphaerostilbe, whilst others have given no indication of such an association. Of Isaria the greater proportion, probably all which flourish on dead insects, are the conidia of Cordyceps.¹ The Phaeostilbeae are more variable in their conidia, being grouped in five sections, as in Dematicae, of which it is the analogue, and they represent a somewhat higher development. Some of the genera exactly correspond to genera of Dematicae, but with a compound stem, as for example Sporocybe and Periconia, Podosporium and Helminthosporium, Sclerographium and Mystrosporium. Instances of undoubted relationship with the higher Fungi are rare, but in some cases it is suspected.

The family of *Tubercularieae* includes genera which recede from the moulds in their compact form, thickish stroma-like base, more or less pustular, erumpent habit, and somewhat gelatinous consistency, which suggest analogies with such genera as Dacryomyces, amongst the Tremellinae. Here again are two parallel sections, the Mucedineae and the Dematicae, in the former of which the colour is whitish, or brightly coloured, and in the latter dusky or black. The subdivisions follow the same plan as in the preceding families, firstly into sections based on the septation of the conidia, and afterwards into genera, or groups of genera, according to the character of the stroma. The typical genus, Tubercularia, with some sixty species, is composed chiefly of the conidia of corticolous species of Nectria, of which a familiar example may be found upon nearly every dead twig of currant bush lying on the ground² (Fig. 132). The whole surface of the twig will be found to be covered from end to end with little bright pink prominences, bursting

² "A Currant Twig and Something on It," by M. C. Cooke, in *Gardener's Chronicle*, 28th Jan. 1871.

¹ See Vegetable Wasps, etc., by M. C. Cooke, London (1892), p. 189.

through the bark at regular distances, scarcely a quarter of an inch apart. Towards one end of the twig the prominences



FIG. 132. — Twig with Tubercularia above and Nectria below. Gard. Chron.

will doubtless appear of a darker colour, almost blood-red, and, intermediate between the two, pink pustules sprinkled with red dots. The dark red pustules are composed of a number of minute red bodies clustered together, the perfected condition of the parasite (Fig. 133). By removing the bark it will be seen that the pink bodies have a paler stem, which expands above into a rather globose head, covered with a mealy bloom. This is the Tubercularia, which at its base penetrates to the inner bark, and there the threads of mycelium branch in all directions, within the bark, but do not extend to the woody tissues beneath. The head, more closely examined, will be found to consist of delicate parallel threads, which are compacted together into a common stem, with its head. Some threads are simple, others branched, bearing here and there little bodies, easily detached, which are the conidia, and form the mealy bloom of the surface (Fig. 134). The darker clusters, when examined in the same manner, will present,

instead of one uniform head, a cluster of smaller globose bodies, closely packed together, or, in some cases, a circle of these dark bodies around a smooth pink centre. These darker bodies are the mature Nectria, which grow at length upon the same stroma, and are the ultimate development of the pink pustules which produce the conidia. Each of the dark bodies is a perithecium, or receptacle, which encloses the fruit, consisting of sporidia, contained in asci (Fig. 133 at G). Here, then, we have the Tubercularia in the first instance, as a smooth, compact, pink, erumpent pustule, the stem composed of numerous delicate threads conglutinated together, and sprinkled with minute conidia; then the darker capsular *Nectria* originates from the same stroma, these capsules containing the fully-developed sporidia enclosed in asci,—the first stage representing the *Tubercularieae* family of the Hyphomycetes, the last stage belonging to the Hypocreaceae family of the Pyrenomycetes. Hence, as the first is an imperfect condition, the Fungi to which it belongs are characterised as *imperfect Fungi*.

We might follow the same process with one or other of

the species of *Fusarium*, which is a genus in the present family, the conidia of which are comparatively large, fusiform, and mostly three or five septate. Some of them are, in like manner, only the conidia of some more highly developed Fungus, and often a species of *Nectria*. The pustules are not so compact, sometimes effused,



FIG. 133.—Tubercularia, D; with Nectria, E; section, F; and asci, G. Gard. Chron.

seldom with a determinate stroma, and rarely with the hyphae much developed. The genus altogether is much more variable



FIG. 134.—B, section of *Tubercularia*; C, conidia. Gard. Chron.

than *Tubercularia*, and not so well constituted, so that possibly it will be broken up into more homogeneous genera in the near future. On the faith of some observations made by Mr. Worthington Smith, the conidia must be regarded as bodies of

a much higher order than their analogues in *Tubercularia*. Not only are they capable of dividing at the joints, and each segment vegetating as a separate unit, but these may be converted into chlamydospores, or at least have a thickened epispore, capable of hibernation. When this is confirmed it will go far towards necessitating a revision of the classification, so far as an association with *Tubercularia* is concerned.

• For the purposes of classification, the genera of the Tuberculariae are grouped according to the general principles adopted in the Mucedines and Dematiaei, and in fact throughout the Saccardian system—that is to say, the sections are based on the septation of the conidia, whether unicellular, bilocular, multicellular, or with stellate or helicoid forms. In each of the sections the genera are characterised by the features presented by the sporodochium, or spore-bed, and the development of the gonidia, whether produced singly or in chains. There are some forty-two genera in all, which it would be somewhat tedious to describe in detail.

The *Tuberculariae Dematieae* contain such genera as possess the habit and development of Tuberculariae, but with coloured hyphae, and similarly coloured, or rarely of hyaline, gonidia. They are less numerous in genera and species than the previous section, but many of the genera correspond in habit and appearance, differing only in the coloured hyphae. Not long ago, when the septation of conidia was not held to be of generic importance, or the coloured or uncoloured hyphae a fact of moment, the few genera which were contained in the Tubercularieae were rather a heterogeneous collection of species, held together by some superficial character, and embracing forms which are now dispersed through several genera. The large increase of genera which has resulted from the adoption of a more precise method of classification is therefore something more than a numerical gain, since it is the result of a closer investigation, and the application of a more uniform and scientific system, which in the end must conduce to the benefit of the student, and, encouraging a more rigid examination of species, tend to the advancement of this branch of biological study.

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CHAPTER XXIV

MICROBES-SCHIZOMYCETES AND SACCHAROMYCETES

THE recognition of the Schizomycetes, or "splitting Fungi," as an order, is of comparatively recent date, and the entire study, notwithstanding all that has been done, is still in an elementary condition. The very minute organisms of which the group is composed have long been recognised, but even now it is open to doubt whether they should be associated with Algae or with Fungi, or outside of both. As part of the Infusoria, Ehrenberg made the first attempt at their classification in 1838. Then they were transferred, almost bodily, to Algae, in 1872, whilst, more recently, they have been held to be most closely related to Fungi, and united to Fungi by Saccardo in 1889. It is of but small import whether they should, technically, be regarded as Fungi or only as allies : they evidently are closely related, and, notwithstanding their minute size, are of too great importance to be practically ignored. They are defined as "unicellular plants, which multiply by repeated subdivision, in one, two, or three dimensions of space, and also frequently reproduce themselves by spores, which are formed endogenously." Mr. Grove points out that they differ from Algae: "On account of their want of chlorophyll they are reduced to live on ready-organised substances, as are Fungi generally. The Schizomycetes, therefore, produce in their substratum, or in the fluid which they inhabit, very considerable and striking decompositions. They perish in pure water containing no decomposable substance. They grow, therefore, exclusively in organic liquids, or in water, or on damp spots, where there is an abundance of organised matter."1

¹ Synopsis of the Bacteria and Yeast Fungi, by W. B. Grove, B.A., London, 1884.

SCHIZOMYCETES AND SACCHAROMYCETES 291

The term "Microbe" has been employed, in a general sense, by the French, and adopted from them to indicate all the minute organisms which are now recognised under Schizomycetes and Saccharomycetes,

whilst in many cases the former are often spoken of simply as "Bacteria" and the latter as "ferments." These "bacteria" appear "in liquids examined under the microscope as small cells of a spherical, oval, or cylindrical shape, sometimes detached, some- FIG. 135 .- Bacterium termo. Chatto and times united in pairs, or in



Windus.

articulated chains and chaplets (Fig. 135). The diameter of the largest of these cells is two micromillimetres and that of the smallest is a fourth of that size, so that at least 500 of the former and 2000 of the latter must be placed end to end in order to attain the length of a millimetre. It is therefore plain that a magnifying power of 500 to 1000 diameters, or even still higher, is required to make these beings clearly visible under the microscope."1

Besides the vegetative multiplication of these cells in one, two, or three directions, there is a double method of formation of spores, which must be described. So long as all the conditions remain favourable to growth and vegetative development, only vegetative multiplication prevails. If the cells can obtain sufficient food, and the food is of exactly the right kind, the rate at which they grow is marvellous. "Cohn calculated that a single germ could produce by simple fission two of its kind in one hour, in the second hour these would be multiplied to four, and in three days they would, if their surroundings were ideally favourable, form a mass which can scarcely be reckoned in numbers-or if reckoned, could scarcely be imagined-4772 billions. If we reduce this number to weight, we find that the mass arising from this single germ would in three days weigh no less than 7500 tons. Fortunately for us, they can seldom get food enough to carry on this

¹ Microbes, Ferments, and Moulds, by E. L. Trouessart, London, 1889.

appalling rate of development, and a great number die both for want of food and because of the presence of other conditions unfavourable to their existence. Vegetative multiplication only takes place when the conditions are extremely favourable to the growth of the organism. If nutrition is interfered with in any way, or if the removal of excretionary products is obstructed, or if there be a large amount of oxygen present, marked changes may at once be observed in the appearance of the protoplasm of the micro-organism. It becomes granular, then a small bright point appears in each cell; this point gradually increases in size until its diameter may be greater than that of the original organism. This large, clear, rounded, ovoid, or rod-shaped node is known as a spore, or resting spore, by which the species may be continued although the parent should perish. The shape varies slightly in different species, but in every case it has a dark limiting outline; it is devoid of colour, and is highly refractile. The dark outline of the spore is usually surrounded by a pale, soft, gelatinous envelope, the substance of which may, in some cases, be accumulated in rather larger quantity near the two poles of the refractile body. As soon as these bodies make their appearance, degeneration of the protoplasm of the bacteria in which they are found immediately follows, but the period at which the death of the protoplasm actually takes place varies in different cases. Where the spores are small they may lie for some time imbedded in the protoplasm of the cell, which, as it degenerates, leaves the resting spore free to be carried about from place to place, by currents of air or water, to be developed when the conditions of moisture, temperature, and food supply again become sufficiently favourable. Where the diameter of the spore exceeds that of the bacterium, it may be situated in the centre, giving rise to a spindle-shaped organism; or it may be at one end, when the organism becomes clubbed or pendulumshaped. The spore in this case appears to escape more readily. This method is that which De Bary has called endospore formation." 1

Another kind of spore is called arthrospore, which is also

¹ Bacteria and their Products, by G. S. Woodhead, M.D., London (1891), p. 33.

SCHIZOMYCETES AND SACCHAROMYCETES 293

defined by De Bary. In this there is a combination of spore formation and of fission; the mother cell undergoes division into a series of daughter cells, a few of which differ from the rest in very important and essential points. There appear to be two kinds of anthrospores : one form, met with in Leuconostoc, for example, where simple vegetative division of small round bacteria goes on regularly, so long as the conditions are favourable, and a regular chain is formed. In this chain there appear at intervals *micrococci*, which differ from the remainder of the elements of the chain in the following points. As soon as the conditions of nutrition are altered they do not, like the other parts of the chain, die off, but they become somewhat larger than the rest, acquire a more distinct outline, become thicker-walled, and their protoplasm grows darker. Eventually they become free by the deliquescence of the gelatinous envelope, and may claim the name of spores, because, when placed in the fresh nutrient solution, they develop into new rows of beads like those of the mother plant. This body has most of the characteristics of the resting spore, but it is not formed within the protoplasm of the vegetative organism, but by a process of fission, and as a result of vegetative division. It is possible that there is as much differentiation of the protoplasm as there is where the spore is formed within the cell, the only distinction being that the separation between the spore and the vegetative element of the chain takes place at an earlier stage, and more completely, than in endospore production. The reverse takes place in Bacterium Zopfii, which, during the vegetative stage, consists of short rods, then of motionless filaments, and, if the temperature be lowered, of short motile As soon as conditions become unfavourable the rods, rods. apparently by a simple process of fission, are divided into short roundish cells, which retain their vitality for a considerable time, and, when placed under favourable conditions, act as spores-that is to say, they develop into the original characteristic rod-shaped bacteria.

The functions of the Schizomycetes have been described as exciting peculiar decompositions, and transforming complicated chemical combinations into simpler ones. This chemical action consists in the production and excretion of

colouring matters, such species being distinguished as *chromo*genous; in the exciting of various fermentations, and hence called *zymogenous*; and in the decomposition of the humours of animal and human bodies, whereby diseases arise, and these are *pathogenous* species. Some authors prefer to group them as pathogenous, zymogenous, and saprogenous.

The classification of this order must still be regarded as imperfect and transitionary, and will be the subject of much change in proportion to the development of knowledge which experience will afford. There are some who are prepared to accept all the morphologically or physiologically distinct forms as different species, and with them the number of genera and species would be large. There are others who hold that most of the Schizomycetes pass through a series of adaptive forms, influenced by surrounding circumstances, and modified by external conditions, so that at one time it may have the form of a Bacillus or of a Bacterium, of a Micrococcus or a Spirochaete. In this latter case the number of genera and species would be reduced to their lowest expression. Perhaps, in the present state of knowledge, the wisest course is to accept the various forms as they appear to be, on the presumption that they are autonomous, and leave condensation and reduction to the gradual operations of the future, and the verification of facts or assumptions, in the light of experience. The arrangement adopted by Saccardo recognises three primary groups, or families. The Trichogenae, with three evolutionary states-the filament, the rod, and the coccus-of which the filament is the primary condition, vaginate or evaginate, fixed at the base or radiating from a central point, rarely entirely free; rods and cocci included in the filaments. The second family, Baculogenae, also with three evolutionary states—rods, filaments, and cocci. In this group the rod is the primary state, the filament secondary, never vaginate, or fixed, or radiating, formed by the indefinite prolongation of a single rod or the union of many. The third family, Coccogenae; there is but one state, that of the coccus. Beyond this it would not be profitable to follow the subdivisions.

No one can doubt for a moment that the pathogenous species are of immense importance as objects of study and

SCHIZOMYCETES AND SACCHAROMYCETES 295

investigation, in face of the contention that in men and animals, and probably plants, they are the associates, and in

many cases the causes, of disease. Since the discovery of the *Bacillus* of anthrax, or splenic fever (Fig. 136), facts have rapidly developed in the association of microbes with contagious diseases, which previously were theoretically attributed to many sources. That which at first was an hypothesis is now an ascertained fact; but before an infectious disease can be considered due to the presence of a



FIG. 136.—Bacillus anthracis. Chatto and Windus.

specific microbe, it must submit to the test of the four rules established by Koch. (1) "The microbe in question must have been found either in the blood or tissues of the man or animal which has died of the disease. (2) The microbe taken from this medium, and artificially cultivated out of the animal's body, must be transferred from culture to culture, for several successive generations, taking the precautions necessary to prevent the introduction of any other microbe



FIG. 137.—Development of the *Bacillus anthracis*. After Ewart.

into these cultures, so as to obtain the specific microbe, pure from every kind of matter proceeding from the body of the animal whence it

originally came. (3) The microbe thus purified by successive cultures, and reintroduced into the body of a healthy animal, capable of taking the disease, ought to reproduce the disease in question in that animal, with its characteristic symptoms and lesions. (4) Finally, it must be ascertained that the microbe in question has multiplied in the system of the animal thus inoculated, and that it exists in greater number than in the inoculating liquid." These conditions have been fulfilled in the case of a large number of diseases, such as anthrax, swine-fever, smallpox, erysipelas, etc., and the microbe theory of the origin of contagious diseases is, in principle, accepted as fact.

The close study and prolonged investigations of pathogenous species led to important results in the practice of a system of vaccination, which has been adopted not only in anthrax but also in other contagious diseases. It has long been known that in a number of diseases of this class one attack carries some immunity against that particular disease in the future. The process had been employed in smallpox, and it was found that vaccination of a mild form commonly ensured the individual, at least for a lengthened period, against subsequent attacks from the virulent form. It was thought to apply this to animals in the case of anthrax, if a mild form could be obtained for the purpose. In 1880 Greenfield announced the first indication of the modification of anthrax virus, and from that time forward there was a steady advance in the production of a protective vaccinal fluid for anthrax. Pasteur attributed the diminution of the virulence of the bacillus to the action of heat, in the presence of oxygen, but Chauveau contended that heat alone was sufficient. By cultivating the bacilli successively in a temperature of from 42° to 43° Cent., they were found to lose all their vitality in about six weeks, this loss going on progressively with the rise of temperature. Sheep inoculated with the culture, after twelve days' heating, only succumbed to the extent of one half. After twenty-four days of heating, inoculation did not cause the death of a single animal. After twelve days more, inoculation with virulent anthrax blood only caused slight febrile conditions. Absolute protection could only be secured by a second vaccination with the attenuated lymph. It was demonstrated further that the modified action of the bacilli was transmitted to their spores, and that, when produced, these sprouted, not into virulent anthrax bacilli, but into modified anthrax bacilli, suitable for vaccination.

It follows, then, that when animals are inoculated with a liquid containing bacilli, of which the virulence has been attenuated by culture, carried as far as the tenth generation, their lives are preserved; they have the disease in a very mild form, and, as a result of this treatment, they are henceforward safe from a fresh attack of the disease,—they are vaccinated against anthrax. Other methods have been tried for the

SCHIZOMYCETES AND SACCHAROMYCETES 297

purpose of modifying the virulence of the original virus, and with more or less of success. As, for instance, a solution of carbolic acid, of one part in six hundred, destroys the microbes, whilst a solution of one part in nine hundred attenuates the virulence without producing spores. Whatever the means, the principle is the same—the reduction of virulence in the bacilli, so as to produce by inoculation only a mild form of the disease.

We have now, writes Dr. Woodhead, "a whole series of diseases from which immunity may be conferred by the inoculation, or introduction into the tissues of an animal of the soluble products of pure cultures of micro-organisms. In America hog-cholera has been vaccinated against, the vaccinator using the sterilised cultures of the hog-cholera organism as his protective virus. Wooldridge, who was the first to adopt this principle in connection with anthrax, was followed by Pasteur and Perdrix, and by Hankin. Fowlcholera, certain forms of septicaemia, and a number of other diseases, amongst which may be mentioned hydrophobia-in which, however, the facts do not belong to quite the same order-all were brought within the same zone, when it was found that the introduction of the sterilised products of a specific organism, first in minute doses and then in gradually increasing doses, could confer a protection against the subsequent action of even the most virulent organism that, under ordinary circumstances, gives rise to the same products as those injected."

The discovery of bacteria in plant diseases is more recent, although Béchamp noticed the presence of microzyma, or bacteria, in the affected parts as long since as in 1869. Still at that time, and long after, they were held to be the associates, and not the cause, of disease. In 1880 Dr. Burrill declared the shrivelling of pears to be due to a species of bacterium, and in 1882 Wakker of Amsterdam attributed the jaundice of hyacinth bulbs to the same cause. In 1885 a bacterium was detected in vines said to be diseased by *Phylloxera*, and affirmed to be the true cause of the disease. More recently still, and the California vine disease¹ was

¹ Gardener's Chronicle, July 1893.

attributed to the presence of bacteria. In 1891 Dr. Halsted¹ apparently determined that a rotting disease of cucumbers and melons was caused by microbes, and that not only could healthy plants be infected, but the virus could be transferred to tomato plants, rapidly producing decay. The destructive "Peach yellows," which long baffled all efforts to discover its cause, has been found to contain these organisms, and efforts are being made to trace its bacteriological relationships. Finally, the pear blight which Dr. Burrill investigated in 1880, and which is sometimes called "fire blight," was finally determined in 1884 to be the result of the attacks of Micrococcus amylovorus, otherwise named Bacillus amylovorus. In this species, although the formation of zooglaea has never been observed in the tissues of the tree, or upon solid media, they occur with much regularity in fluid cultures, when placed under favourable conditions for rapid growth. They are produced to some extent throughout the fluid, but are most abundant in the thin pellicle which forms upon the surface. They often appear the more distinctly by being surrounded by a colourless layer, free of bacteria, which is an extension of the basal stratum of the zooglaea mass. This branch of the inquiry is, however, of such recent origin, and is in such elementary condition, that it would be imprudent to affirm too much, or indulge too freely in speculation.

Thus much, then, for the Microbes, which are regarded generally, and spoken of, as the organisms which are instrumental in producing putrefaction. It is remarkable what a voluminous literature has already accumulated, within a few years, which may be accepted as some evidence of its importance. The subject may not affect business interests so much as the cognate one of the Fungi of fermentation, but it is more than suspected that it has a very intimate relation to life and death.

The yeast Fungi are very simple and low forms of vegetable life, although of a more imposing size than the *Schizomycetes*, or Microbes, to which we have given brief attention. The yeast Fungi, which are the agents of fermentation, are represented in old books under the name of *Torula cerevisiae*, and

¹ Gardener's Chronicle, 3rd June 1893.

SCHIZOMYCETES AND SACCHAROMYCETES 299

the generic name of Torula prevailed, in all notices of yeast plants, for very many years after it was demonstrated and known that Torula had nothing whatever to do with them.

> But faith, fanatic faith, once wedded fast To some dear falsehood, hugs it to the last.

The cells, in budding, give rise to similar cells, attached to each other in chains, resembling the conidia in Oidium, or, less closely, those of some species of Torula, in which latter genus the cells are dark coloured, almost black. The similarity of form led to the confusion of names; whilst in point of fact the yeast Fungi have no affinity with Torula.

The technical, or scientific, description of the yeast Fungi is "Unicellular plants, which multiply themselves by budding, and reproduce themselves by endogenous spores. They live singly or united in bud colonies, chiefly in saccharine solutions, where they excite alcoholic fermentation." For the purpose of illustration, the yeast which causes fermentation in beer may be taken as a type of these organisms. Primarily they consist of a single cell, which is round or elliptic, but occasionally becomes elongated, and parted off by transverse divisions. In order to multiply themselves, the simple cells produce an outgrowth from the periphery, which gradually

enlarges, absorbs a portion of the contents of the parent cellwhich it ultimately resembles in form and size-then the connection between them is cut off by a transverse wall or partition, and two cells occupy the place FIG. 138 .- Saccharomyces ellipsoideus. of the former one. Each of



Chatto and Windus.

these cells is capable, in like manner, of budding and producing daughter cells, and so the course goes on (Fig. 138).

Increase by budding, or gemmation, goes on most rapidly under the influence of moisture, mostly immersed in a saccharine solution, and in this position the sugar of the fluid is decomposed, resulting in alcoholic fermentation. Spores may be developed on a moist substratum, by the contents of a cell dividing itself into two or four portions, each of which

surrounds itself with a proper membrane, and becomes a spore, which is capable of budding, like the vegetative cells.

Whether the so-called species of Saccharomyces are autonomous, or only stages in the development of some higher forms, need not be discussed here. "Brefeld considers that the conidia of various species of Ustilagineae exactly resemble in mode of growth many of the forms of the so-called Saccharomyces. It is well known that the spores of the smuts, in germinating, protrude a thread, from which spring tufts, or clusters, of sporules; these unite with one another by short transverse processes, and then give rise to sporules, or conidia of the third generation, and these to even a fourth kind. Brefeld's theory is that these successive generations of conidia do not merely resemble Saccharomyces, but are identical with them. He cultivated the spores of many Ustilagineae in nutrient fluids, and found that the conidia to which they gave rise were in form and dimensions similar to those of the various species of yeast Fungi-those of one being ovate, of another oblongovate, of another fusiform, of another cylindrical, of another small and roundish, and of another filiform, and so on. Moreover, he cultivated these sporules in suitable media for numerous generations, and found that they reproduced themselves, so long as the conditions remained unaltered, with unfailing certainty the whole year through. A pair of smut spores was induced to germinate, and the conidia which they produced were transported, with due precautions, into a drop of nutrient fluid, in which they continued to bud till the nutriment was exhausted. A few of these were then removed to another drop of the same fluid, and the process was continued for nearly thirty times, extending over a space of twelve The author considers that he has thus proved that months. these conidia can propagate themselves indefinitely by budding, just like the cells of Saccharomyces, and he asks-If we had commenced this series of cultivations, not with the smut spores, but with the conidia which arise from them, should we have been able to distinguish their mode of growth from that of the yeast of beer ?"1

¹ Synopsis of the Bacteria and Yeast Fungi, by W. B. Grove, B.A. (1884), p. 81.

SCHIZOMYCETES AND SACCHAROMYCETES 301

All saccharine fluids which contain glucose, or grape sugar, or a sugar which can be changed into glucose, and also all nitrogenous substances, phosphates, and ammoniacal salts, produce alcohol at a given temperature. The process of conversion is by fermentation. Pasteur states that every fermentation has its specific ferment; in all fermentations in which the presence of an organised ferment has been ascertained that ferment is necessary. This minute being produces the transformation which constitutes fermentation, by breathing the oxygen of the substance to be fermented, or by

appropriating for an instant the whole substance, then destroying it, by what may be termed the secretion of the fermented products.



FIG. 139 .- "High yeast." Chatto and Windus.

Three things are necessary for the development of the ferment—nitrogen in a soluble condition, phosphoric acid, and a hydrocarbon capable of fermentation, such as grape sugar. The common ferment of wine has elliptical cells, but there are other forms, or species, which are capable of producing fermentation in wine. The yeast of beer has round or oval cells,¹ and so on, through the range of species, of which Saccardo enumerates thirty-one (Fig. 139).

It was contended at one time that these ferments were derived from moulds and Mucors, which under favourable conditions continued to increase themselves by budding—viz. simple vegetation—but, if deprived of nutrition, produced the fructification of a mould. De Bary, whilst controverting this, suggests that some yeast cells have probably been mixed with the spores sown in a nutritive fluid. He thus describes the development of yeast, beyond the ordinary vegetation in a fermentable solution : "If we bring living cells of yeast out of the fluid, on the moist surface of a succulent part of a plant for example, a piece of carrot—the sprouting goes on slowly for some time, and entirely ceases after some days. About the sixth day, we remark how some of the cells wither and others

¹ Microbes, Ferments, and Moulds, by E. L. Trouessart, London, 1889.

become larger; the greater part of the latter form spores in their inner space through the free formation of cells, like those of an ascus, and then becoming thicker at the cost of the protoplasm, at last entirely fill the membrane of the utricle. We can produce the same phenomenon if we thoroughly wash fresh yeast, and, mixing a little clear water with it, let it stand. The formation of the spores here follows, by a sufficient supply of water, at the cost of the organic substance, which has assimilated during the fermentation; we must seek it in the yeast which is used technically when, after its fermentation is complete, it is laid aside clear and wet. The spores begin, when they are brought into a suitable liquid, to sprout like the vegetating cells, in order to produce new repeated generations of the latter. No other forms of development are known for the Fungus which is found in yeast."¹

The yeast Fungus is the principal promoter of the alcoholic fermentation which appears in practical life, especially the greater part of beer and spirit fermentation. That which is distinguished by the name of barm, and the yeast deposited at the bottom of the cask, are in many cases-not in all-the same Fungi, which in a lower temperature remains at the bottom, and collects as under-yeast; by higher temperature it accumulates in the froth on the surface of the fluid, and is called *barm*. There is a slight difference in the form of the yeasts, but the one form can be transferred to the other, by changing the temperature of the fermentation. Further details will have to be sought in some work dealing specially with the subject, as we are only interested in furnishing an outline of the organisms concerned in the processes of putrefaction and fermentation.

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303

CHAPTER XXV

SLIME FUNGI-MYXOMYCETES

THE Myxomycetes, or Myxogasters, are an extraordinary group. which have been the subject of much discussion, on account of some peculiar features which characterise them, and separate them from Fungi generally, and all other of the Cryptogamia. On this account some have advocated their exclusion from the vegetable kingdom altogether, whilst zoologists have been in no hurry to accept them. The common error of accepting analogy for affinity is one which even scientific minds are occasionally betrayed into committing, and yet, apparently, unconscious of their own failing. We have, during a period of half a century, seen several hypotheses started on similar unstable bases, flourish awhile, and then come to nought. For a long time, and up to a very recent date, the Myxogasters were classed with the Trichogasters, as two groups of the order of Gasteromycetes. Without a knowledge of their life-history, and but little of their microscopical structure, this assumed alliance was a natural one, but it has come to be renounced. It was only in 1864 that the position was assailed by De Bary, who changed the name to Mycetozoa, and claimed for them a position as nearly related to the animal as the vegetable world. "I have," he says, "placed the Myxomycetes, under the name of Mycetozoa, outside the limits of the vegetable kingdom, and I still consider this to be their true position." Strangely enough, however, in all his subsequent botanical works, he continues to include the Mycetozoa, as if he lacked the courage of his opinions; and other botanical writers and compilers of text-books have continued the same course. In this group the two stages or phases of life, the vegetative and the reproductive,

SLIME FUNGI-MYXOMYCETES

305

are sharply defined and distinct. It is in the vegetative stage that all the supposed affinities with the animal world are encountered, and in the reproductive everything is suggestive of Fungi, even to the terminology which is borrowed from, and represents identical structure with what is familiar in Gastromycetes. The outer wall is either a sporangium or peridium, the threads of the interior still compose a capillitium, the continuation of the stem into the interior is a columella, and the reproductive units are not ova, but the spores. This is accounted for by De Bary from the "close agreement in structure and in biological characters between their organs of reproduction and the spores of Fungi." As Mr. Massee has lately pointed out, it is clear that De Bary derived all his reasons and his evidence against the vegetable nature of the Myxomycetes from the early, or vegetative, phase. On the other hand, it seems to have been suggested that in the later, or reproductive, phase the disparity is so great between the structure and biological characters of the Mycetozoa and those of any of the lower animals, that he was compelled to use the terms, in describing them, which belong also to the Gastromycetes. Here, then, we are supposed to come face to face with a problem-certain organisms in their early, or vegetative, stage belonging to the animal kingdom, and subsequently in their final, or reproductive, stage undoubtedly vegetable,---a worse example of a dual-hypothesis than that which combines an Alga with a Fungus to produce a Lichen.

Taking away all expletives, and reducing the indictment to its simplest form, it remains as a specific reason that "the characteristic mark of separation lies in the formation of plasmodia, or aggregation of swarm-cells." In his recent monograph of this group,¹ Mr. Massee has faced and combated the position occupied by De Bary, step by step. "In the Myxomycetes," he says, "the spores on germination give origin to one, two, or more naked cells, which possess the power of movement, due to the protrusion of pseudopodia, or the presence of a cilium; these cells are known as swarm-cells. The swarm-cells possess a nucleus, multiply by bi-partition, and eventually coalesce to form a plasmodium in the following manner. After the production of numerous swarm-spores by repeated bi-partition, little

¹ Massee, Monograph of the Myxogastres, London (1892), p. 5.

groups are formed by the close approach of two or more of these bodies; these groups often disperse again, but eventually the components of a group coalesce, and lose their individuality : this coalescence and loss of individuality results in the formation of a small plasmodium, which, in some unknown way, possesses the power of attracting surrounding free swarm-cells; these at once coalesce and add to the bulk of the plasmodium. The nuclei of the component swarm-cells retain their individuality in the plasmodium, the latter retaining the power of motion originally possessed by its components, and represent the vegetative phase of a Myxogaster. Under certain conditions, unfavourable for active vegetative work, plasmodia possess the power of passing into a temporary sclerotioid, or resting stage; the preliminaries for this condition are the breaking up of the protoplasm into innumerable roundish or polyhedric cells. In some species the cells become surrounded by a distinct, colourless membrane, which shows the reaction of cellulose."

From the above account we learn that the coalescence of naked motile cells, or even the aggregation of naked motile cells without loss of individuality, is, from De Bary's standpoint, the proof that the Myxogasters are not plants.

After comparison of these phenomena with similar analogous instances in the Phycomycetes and other Fungi, the following reasons are adduced in support of the vegetable, rather than animal, nature of these organisms :—

(1) Frequent presence of cellulose in the general membrane protecting plasmodia, cell-walls of spores, sporangia, and walls enclosing the protoplasm in the sclerotioid, or resting stage of plasmodia. (2) Presence of germ-pores in the cell-walls of the (3) The frequent separation of lime spores, of some species. from the protoplasm at the commencement of the reproductive (4) The frequent separation of a substance from the phase. protoplasm during the period of spore-formation, homologous with the substance separated during the same period in the This substance in the Myxogasters forms Ascomycetes, etc. the capillitium. (5) The agreement with many Fungi in the contrivance for spore dissemination. (6) The production by free cell-formation of spores protected in the early stage with

SLIME FUNGI-MYXOMYCETES

a wall of cellulose, which eventually becomes differentiated, and, as stated by De Bary, "behaves towards reagents in a similar manner to cuticularised plant cell-membranes, and to sporemembranes as in the Fungi. (7) Presenting analogy with undoubted members of the vegetable kingdom, as *Hydrodictyon*, where the naked motile swarm-cells coalesce to form a caenobium, which eventually becomes invested with a membrane. (8) In the close affinity with *Ceratium* (but, as *Ceratium* has been included by some with Myxogasters, this will not carry so much weight). (9) In the coalescence of the naked cells to form a plasmodium, being the result of conjugation between the component cells, thus presenting features in common with the primitive forms included in the group *Zygosporeae*."

It may be added that, in this country, Mr. Saville Kent, as a zoologist, espoused De Bary's views, and even went beyond him, in his *Manual of Infusoria*, for he included the Mycetozoa, and suggested their affinity with sponges. These views were contested at the time,¹ but really no fresh evidence was produced in support of the views of De Bary, who was the great authority cited.

The only addition necessary to quote, or allude to, in support of the animal nature of the Myxomycetes, in the *vegetative* stage, is the evidence of Mr. Lister; but these observations extend no further than the vegetative stage, and do not furnish any convincing proof that the phenomena are incompatible with a condition of vegetable organisms, any more than the amoeboid forms in such Algae as the *Volvocineae*.

"I have repeatedly seen bacteria taken by swarm-cells of Chondrioderma difforme in the manner described, and it would appear that bacteria form their principal food. On one occasion I had a favourable opportunity for observing the digestion of bacilli on account of the quiescent state assumed by a swarm-cell, which remained with little active movement for an hour and a half. On the previous evening I had placed some spores of Chondrioderma difforme in water, under a thin cover-slip; on the following morning swarm-cells were in great abundance in the pure water. I introduced a drop containing multitudes of bacilli from a glass in which a piece of ¹ "Animal Nature of Myxomycetes," in Grevillea, vol. ix. (Dec. 1880), p. 41.

307
Stereum hirsutum had been soaking for several days. In a short time a number of the swarm-cells were seen, attended by bacilli, some of which were attached to their pseudopodia, and some were already enclosed in vacuoles. The swarm-cell in question had taken an amoeboid form, occasionally producing and again withdrawing the cilium, while from time to time thin pseudopodia were extended from the opposite end, but more frequently the posterior region expanded into a somewhat funnel-shaped mouth. Into such an expansion a stout bacillus was seen to enter; in the course of a few seconds it was enclosed with a noticeable amount of water, by the folding over of the lips of the funnel, and conveyed into the body-substance; a few minutes after, another bacillus was taken in, much in the same manner, but no globule of water was introduced. Ten minutes later a large bacillus was caught by a prolongation of one side of the funnel, and in the course of half a minute a tube-like extension of protoplasmic substance invested the bacillus, and it was drawn in. It remained for a short time in direct contact with the granular matter of the body, but was soon surrounded by an oval vacuole. The swarm-cell continued inactive for nearly an hour, when it assumed an extended form, and shortly after swam away with rapid jogging movement. Constant observation was maintained during this hour, and the bacilli were seen gradually to dissolve in the vacuoles in which they lay, until at length all trace of them had disappeared, together with their containing vacuoles, and only the contracting vacuole remained in the homogeneous granular substance of the swarm-cell.

"At the commencement of the observation this granular protoplasm was much more turbid than at the close, when it was remarkably hyaline; the swarm-cell appeared also to have increased in size, though it was difficult to determine by measurement in consequence of its changing form. No rejection of refuse matter took place while the observation lasted.

"In the same preparation I watched a swarm-cell creeping in a straight line, with the strange snail-like movement so difficult to understand. In its course it came to a small group of motionless bacilli lying against the glass; immediately it changed its linear form and spread itself out, covering four of the bacilli. In about two minutes it resumed its former shape and movement, and crept away, carrying off two of the bacilli in vacuoles.

"These observations seem to confirm the opinion of De Bary that the organisms under consideration should be classed among the animal rather than the vegetable kingdom. When a creeping swarm-cell is watched, with the projecting cilium placed immediately in advance of the nucleus, which never shifts its position, and when we note the manner in which the vibrating extremity of the cilium appeared to detect the presence of the bacilli, before the swarm-cell spread itself over

them; again, when we observe the creeping action suddenly change, and raising itself from the decumbent attitude, with a few lashing strokes of the cilium the swarm-cell releases its foothold and swims away; and when to these remarkable



FIG. 140.—Cluster of Tubulina cylindrica.

movements is added the process of ingestion, we cannot but feel the force of the conclusion at which De Bary arrived, if indeed a distinct line of demarcation between the two kingdoms can be said to exist."¹

Nearly all the species in this group are minute, and when not so are composite, several individuals being united in a cluster (Fig. 140). Most of them are more or less gregarious, and sometimes covered with a shiny envelope, of which portions extend to the matrix, and resemble when dry a sort of membranaceous thallus. The tendency is certainly towards the globose in form, now and then attenuated into the cylindrical. If we were to attempt a kind of typical description, we should say that they are small globose or pear-shaped bodies, with or without a stem, scarcely exceeding a millimetre in diameter, variable in colour, sometimes shining and sometimes covered with white chalky granules; at first pulpy, then dry and fragile, filled within with a mass of pulverulent spores, often mixed with threads of a capillitium. Into this interior the stem is continued as a columella, which is connected with the

¹ "Notes on Chondrioderma difforme," etc., by A. Lister, in Annals of Botany, iv. (May 1890), p. 281.

walls of the sporangium by the radiating threads of the capillitium. It will be observed how closely these details accord with those of the Lycoperdaceae amongst puff-balls, so that we would seem to be describing very microscopical puff-balls. To a certain extent this is correct, but with the exception that the early condition is slimy, there is often when mature a thin film of dried mucilage derived from the envelope, and the capillitium is sometimes very highly developed. We must, however, guard against the inference that there is any true affinity between Myxomycetes and Gastromycetes, as old authors believed. They are mostly developed upon dead leaves, or very rotten wood, in damp places; and though probably most common in temperate regions, a few species extend into the tropics.

The total number of recorded species, included in the most recent work on the subject, is 425; but no extended analysis of their geographical distribution has been attempted, as it is not clear that species recorded from distant stations twenty or thirty years ago were determined with sufficient accuracy.

It is unnecessary to allude at any length to the classification adopted for the arrangement of this group. Previous to the Monograph by Rostafinski¹ all the species were arranged according to external characters, determined by the aid of a Although it must be admitted that Fries pocket lens. exhibited a remarkable insight into the relations and affinities of the various groups of Fungi, yet his method was insufficient for the minute species, and the Myxogasters, amongst others, received only inadequate treatment at his hands, so that a revision, with the aid of the microscope, became an absolute necessity. De Bary evidently intended to do this, but never accomplished it, although subsequently one of his pupils, who had the benefit of becoming acquainted with his views, produced, in Polish, the Monograph above alluded to. Rostafinski accepted, in name, the Mycetozoa of De Bary, but with a more restricted application, and his classification proceeded on a botanical basis, since it was the reproductive phase, or completed condition, which he recognised as the individual.

· Sluzowce, a Monograph of the Mycetozoa, by Dr. Joseph Rostafinski (in Polish), 1875.

SLIME FUNGI-MYXOMYCETES

Hence we find that the primary division into two subdivisions was based upon spore characters. In the first section, the *Amaurosporeae*, the spores were violet, or brownish violet; and in the second subdivision, the *Lamprosporeae*, the spores were variously coloured, but never of any tinge of violet. The next feature which seemed to him most important, or at least most fitting for the purpose of classification, was the presence or absence of a capillitium. Subsidiary to these two features, the presence or absence of lime in the sporangium or capillitium, the production or suppression of a columella, and the perforation of the walls, were employed in the delimitation of families; after which followed the genera, with their varied predominant characteristics.

Subsequent writers, having Rostafinski's work as a basis, have proposed alterations and emendations, whilst the majority of mycologists have felt that, although it did much to direct inquiry into 'a new channel, and classify on sounder principles, the Monograph did not exhaust the subject, but left many occasions for improvement. As we are writing this chapter, the latest attempt at a revised classification has issued from the press.¹ In this arrangement the primary subdivision, as to spore coloration, is abolished, and another central idea established, which is thus explained :—" The most pronounced feature in the evolution of the Myxogastres is in connection with spore dissemination, and the following arrangement is based on the relative development of the capillitium, which is seen in its most perfect form in the genera *Trichia* and *Areyria*."

The entire group is subdivided into four orders, in the following sequence:—(1) Wall of sporangium without lime; capillitium absent, or formed from the wall of the sporangium. (2) Wall of sporangium still without lime; capillitium originating from a central columella. (3) Wall of sporangium with an external deposit of lime; capillitium present. (4) Wall of sporangium without external deposit of lime; capillitium present, but not springing from a columella. In the introduction the above is the sequence of orders, but in the

¹ A Monograph of the Myxogastres, by G. Massee, London, 1892; and subsequently that by A. Lister in 1895.

subsequent elaboration the last two orders are transposed. For the most part the genera are the same as in Rostafinski, with the exception of two or three instances in which contiguous genera are amalgamated.

It must be expected that an evolutionist, such as Mr. Massee confesses himself to be, would have decided ideas as to the evolution of this group. "I consider," he says, "the Myxogastres as illustrating one of the earliest known attempts at differentiation in the direction that has eventually resulted in the mass of organisms constituting the vegetable kingdom; but having originated from the Flagellatae, a group more in touch with the animal side of life, the work of developing individuality has been slow, as illustrated by the tardy appearance of cellulose cell-walls, which, as would be expected, is most complete in the newly evolved reproductive phase, itself to a great extent the outcome of a gradual change of environment from aquatic to aerial; but the radical mistake, after having adopted the plant line of development, consisted in the non-development of chromatophores, and retention of the animal mode of nutrition, which in the plant world means parasite or saprophite. The fungi, a later group, differentiated from ancestors that had already evolved the leading plant characteristics, including cell-walls, chlorophyll, starch, hence in this respect are more typical plants than the Myxogastres, but in the fungi, the check to progress was due to the degeneration of the chromatophores, already evolved by their ancestors, whereas, in the Myxogastres, the check was due to their inability to differentiate these essentials."

As for ourselves, we are by no means disposed to dogmatise on any speculations of this kind, which seem to have such a slight basis of solid fact, and permit such a free scope to inference. Neither are we content to exclude Myxomycetes from Fungi, as the above quotation suggests, since their strongest affinities when mature appear to be with Fungi; but we confess to a predilection for regarding them as a peculiar and aberrant group, which, by reason of their vegetative phase, do not fall well into place with our present arrangement of Fungi.

It is incumbent upon us to append a brief synopsis of the

classification which has been adopted for these singular organisms, the characters for which are derived from the final and reproductive condition.

The first of the four orders, into which the entire group is subdivided, is the *Peritrichiaceae*, in which the wall of the sporangium is not encrusted with lime, and the capillitium is either absent or formed from the wall of the sporangium. This order is again subdivided into two suborders—that of the *Tubulinae*, in which the wall of the sporangium is not perforated; and the *Cribrariae*, in which the wall of the sporangium is perforated.

The principal genus in the Tubulinae is that of *Tubulina*, in which the sporangia are crowded

together so as to form an aethalium, which term is applied to an agglomeration of sporangia. The *Cribrariae* includes the genera Enteridium, Clathroptychium, Cribraria, and Dictydium, in all of which the perforated sporangia are very elegant objects. The subsidiary characteristics of the several genera have reference chiefly to the manner of the perforations. In Cribraria the permanent upper portion of the sporangium forms a



FIG. 141.—Cribraria intricata.



FIG. 142.—*Dictydium*, natural size and magnified.

kind of network (Fig. 141), and in Dictydium the permanent radiating ribs are united by transverse bars (Fig. 142).

The second order, *Columelliferae*, with the walls of the sporangium not containing lime, has for its chief character a central columella, from which the capillitium originates. The two suborders into which this group is divided are the *Stemoniteae*, in which the capillitium springs from every part of an elongated columella,

and the Lamprodermeae, in which the capillitium springs from



In the Stemoniteae the typical genus is Stemonitis (Fig. 143), in which the sporangia are free, whilst in the other genera, as Amaurochaete, Brefeldia, and Reticularia, the sporangia are combined into an aethalium. In the other section, called Lamprodermeae, there are some half dozen genera, in all of which the sporangia are free, but in the most numerous and typical genus, Lamproderma, the threads of the capillitium arise from the abrupt apex of a short columella.

The third order is the Lithodermeae, which includes a great number of species, and is subdivided into two sections, in both of which there is an external deposit of lime on the wall of the sporangium. The Didymeae have a capillitium which is wholly without lime (Fig. 144), and the *Physareae* a capillitium which encloses lime. We need not stay to analyse the different genera in these two sections, inasmuch as they will offer no difficulty to the student. The Didymeae includes such genera as Chondrioderma, Didymium, Lepidoderma, Spumaria, and

Diachaea (Fig. 145). In Spumaria only are the sporangia combined in an aethalium, in each of the other genera they are free. The typical genus, Didymium, has the sporangium encrusted with a powdery coating of lime, and the distinguishing feature of



FIG. 144.—Didymium farinaceum.

the three other genera consists in the coating of the sporangia. The Physareae include eight genera, only one of which, Fuligo, has the sporangia combined into an aethalium, as a generic character, although in other genera some of the species may form an aethalium. Physarum is a large genus in which

SLIME FUNGI-MYXOMYCETES

the capillitium is much swollen at the nodes, enclosing lime; whilst *Tilmadoche* has small nodes containing lime, and *Badhamia* has thick threads in the capillitium, containing lime throughout. In *Craterium* the form of the sporangium more or less resembles a wine-glass, closed by a lid or operculum



FIG. 146.—*Craterium*, natural size and magnified.

spores of Trichia.

(Fig. 146). The remaining genera are small, consisting of a single species in each.

The last of the four orders is the *Calotricheae*, in which the capillitium is for the most part highly developed, and the sporangia have no external deposit of lime. The two subdivisions are

Tricheae and Arcyriae; in the former the threads of the capillitium are free, and do not anastomose, whilst in the latter they are attached by one end, IG. 145.— Diachaea, with capillitium and columella exposed.

or combined into a network. The Tricheae include two genera, the principal being *Trichia*, in which the threads are spiral



FIG. 148.—Arcyria, with portion of capillitium magnified.

(Fig. 147), and *Oligonema*, in which there are no distinct spirals. The seven genera of the *Arcyriae* are partly known by the character of the capillitium, of which the largest genus is Arcyria, having the threads combined into a network which becomes naked or protruded at maturity (Fig. 148). Two other genera,

such as Lycogala and Perichaena, have elementary threads, and the remainder are of secondary importance. This is, briefly, the basis of classification in the Myxomycetes, and is dependent, as in other groups, upon the full and mature development of the individuals for their identification.

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PART III

DISTRIBUTION



CHAPTER XXVI

CENSUS OF FUNGI

THE estimated number of species in any department of natural history, at any given time, is of passing interest, although necessarily it is always changing, and must, to a great extent, be only an estimate. It is a very long time since any estimate of the number of described species of Fungi could have been made upon an equally satisfactory basis to the present. This is due to the recent publication by Professor Saccardo of a *Sylloge*, which was presumed to contain an enumeration of all species described up to date, and this *Sylloge* must therefore be taken as the basis of our calculations.

The last previous attempt at a full enumeration of species was that of Streinz' Nomenclator, dated 1862, in which the total number of species was 11,893; and besides that we had only vague estimates to guide us, such as that expressed by De Bary in 1872, when he said, " It is no exaggerated estimate, if we place the number of the species of living Fungi on an equality with that of the floriferous plants, viz. about 150,000." Probably his intention was not to include merely the described species, which had been discovered, but to estimate the entire number of species, known or unknown, which might be in existence on the surface of the globe. After all, such an estimate could only have the value of an individual opinion. An estimate which we ventured to give in about 1872 placed the number of known species at 20,000; whilst, some fifteen years afterwards, we intimated an opinion that they must approach to nearly double that number; whereas a clear total, according to Saccardo, on a determinate basis, is 40,000 up to 1892. It is interesting to revert to the opinions and estimates

of some still earlier writers than we have mentioned. Humboldt, for instance, three-quarters of a century ago wrote : "If we estimate the whole number of the Cryptogamia hitherto described at 19,000 species, as has been done by Dr. Klotsch. a naturalist possessing a profound acquaintance with the agamic plants, we shall have for the Fungi 8000 (of which the Agarics constitute the eighth part)." It is a remarkable coincidence that in Saccardo's enumeration the Agarics still constitute the eighth part of the whole. As to the Hymenomycetes, which include the Agarics, Fries, in his Humenomycetes Europaei, gives a total number of species for the whole of Europe as 2778. Before the publication of the Sylloge, we remarked on this fact: "It may fairly be concluded that the total number of species of the Hymenomycetes is not less than 5000." Subsequently the Sylloge extended that number to 9634, the proportion of which that are confined to Europe we have not ascertained, but it is considerably beyond that enumerated by Fries. The total of species of Hymenomycetal Fungi now known reaches to nearly one-fourth of the total of described species of Fungi. If we analyse these results still further, we find that of the Hymenomycetes not less than 5245 belong to the Agaricini, or gill-bearing series, and 2200 to the Polyporei, or pore-bearing series, leaving only rather more than 2000, or about equal to the whole of the Polyporei, for the remainder of the Hymenomycetes, i.e. the Hydnei, Thelephorei, Clavariei, and the Tremellini.

The next group of importance, as to number, is that of the *Pyrenomycetes*, formerly termed the *Sphaeriaceae*, in which the spores are contained in asci and enclosed in a perithecium. Placing the total at 10,500, we see at once that it is more numerous in species than the whole of the Hymenomycetes, and more than one-fourth the total of all known Fungi. It must be remembered that the largest perithecium known is not much larger than a grain of mustard seed, or, at any rate, not so large as the seed of a vetch, although in some compound species, in which some hundreds of perithecia are collected in a single stroma, that stroma may attain the size of a man's fist. Hitherto the number of British species has always been less than the total of British Hymenomycetes, perhaps

not more than three-fourths, but recently the difference has diminished.

Closely allied to the above are the Discomycetes, with the sporidia also enclosed in asci, but with the fertile disc exposed. The species enumerated are about 3800, with which there are no previous lists for comparison, and no estimate, save that of twenty years ago, when we estimated the total number at something like 2000 species. The Systema of Fries only contains about 430 species for 1822; whilst for British Discomycetes alone, Phillips, in 1887, records 607 species. A large majority of the species are fleshy, and hence almost confined to temperate regions, but it is only during recent years that they have been studied seriously and effectively. Until about twenty-five years ago they were absolutely neglected, and we are indebted chiefly to Fuckel, Nylander, and Karsten for indicating the lines upon which future studies should be pursued.

The remaining groups are comparatively small, and none are of more importance than the Gastromycetes, which are of considerable size, so as not to be easily overlooked, and distributed over a wide geographical range; yet the number of species has hardly increased in proportion to those in other groups. The present total number of species, of all kinds, does not exceed 720, and of these no less than 173 are represented in Australia, which seems to be the happy land for the Gastromycetes, not half that number being found in

The Hypodermei include the two smaller groups which are better known as the Uredinei and the Ustilaginei, to both of which large additions have been made in recent years, not so manifest in a catalogue on account of the union of the members of several so-called genera under one designation. Some of the present species are by no means stable, which go to make up the total of 1750. The Ustilaginei only number about 320 of these, leaving 1430 species for the Uredinei. total number of British species, according to the latest mono-The graph, was 261. The previous catalogue for 1878 included 293 species, but this is accounted for by the new arrangement placing the Aecidium, Uredo, and Teleutospores under one generic denomination. This makes it difficult to compare

recent lists with old ones, although practically a considerable increase is inevitable.

The *Phycomycetes* are interpreted now in a broader sense than they were a few years ago, which renders comparison with the older authors difficult; nevertheless we must accept the 686 species which are included in the total of the *Sylloge*.

We have still upwards of 10,000 species to deal with, which belong to the imperfect Fungi, and these include 6865 which are classed under the *Sphaeropsideae* and *Melanconiae*; and 4760 moulds or *Hyphomycetes*. Although these are suspected to represent imperfect states of other Fungi, they must retain a place as species until their affinities are determined. Undoubtedly the number of these form-species has increased enormously of late years; they have always held a subsidiary place in the estimation of mycologists. Certainly a combined total of not less than 1400 species may be set down as British, against 489, the total number recorded in the *Handbook* for 1871, or nearly treble within about twenty years.

Whatever position posterity may assign to the Microbes, they cannot be excluded from our census. Hence we have a record of no less than 689 species of *Saccharomycetes* and *Schizomycetes*, otherwise known as yeast Fungi and Bacteria, which are absolutely the growth of the past few years. There are some who are ready to contend that the bacteria are all, or nearly all, simply the modifications of a single species; but there is such a thing as rushing to extremes, so that whilst we may cherish the belief that more experience and closer observation will tend rather to diminish than increase the number, we must accept the total as it stands. There are no standards for comparison that are twenty years old, and in Britain the first attempt to construct a synopsis was not made until 1884, and even in this the indigenous species are not indicated.

Finally, the slime Fungi, or *Myxomycetes*, have to be included, for we do not hesitate to regard them as more closely related to Fungi than to anything else, and of these there are 450 species. They do not increase so rapidly in numbers as some other groups, and we have a very good standard of comparison in Rostafinski's *Monograph* of 1875, which enumerated 178 species. Of these no less than 100

CENSUS OF FUNGI

were identified as British in 1877, and that number was increased to 144 by Massee in his *Monograph* of 1892. There are one or two smaller groups which could scarcely be included in any of the principal groups, but they do not altogether exceed more than about some 200 species.

From the foregoing, then, we gather the following conclusions—that the total number of described species of Fungi to 1892 was about 40,000.

Of the Hymenomycetes we accept a total of		0.004
For the Pyrenomycetes, or Sphaeriaceae	•	9,634
To these add for the D:		10,500
To these add for the Discomycetes		3,800
And for the Gastromycetes		
The Hypodermei on Pust and G	•	720
The Hypodermei, or Rust and Smut Fungi		1,750
The Phycomycetes in its broadest sense		686
The Sphaeropsideae and Melanconiaceae		
The Hyphomycetes, or Moulds	•	6,865
The Saccharomycetes and Schizomycetes		4,760
The Massacharomycetes and Schizomycetes		689
The Myxomycetes, or Slime Fungi		
Tuberaceae and others not specialised .		450
	-	145

CHAPTER XXVII

GEOGRAPHICAL DISTRIBUTION

THE facts from which a satisfactory account of the distribution of Fungi over the world could be constructed are, even now, too fragmentary for the purpose. For the more civilised and best known countries there is not much difficulty, but there are still immense tracts over which no mycologist has ever passed, and for which no catalogue of species is known. When we attempted a survey of this kind twenty years ago, we were perfectly conscious of this difficulty, and in that interval very few of the difficulties have been removed. Although the materials are more complete than they have ever been for generalisation in respect to well-explored countries, it is unfortunately true that very few of the countries then imperfectly known, or wholly unknown, in this respect are in a better position now than they were then. Even in Europe we are still compelled to confess ignorance, almost as great as it was then, of the whole of European Turkey, a great part of Russia, and the Spanish Peninsula. And this forms the stronger contrast on account of the better development of our knowledge respecting the remaining countries. In the northern parts of the New World there has been continued activity, excepting in those parts which are under British rule, where no progress has been made. Of all the vast continent of Asia we are nearly as ignorant as we were a quarter of a century ago. For Japan there is a prospect of a better future through the exertions of a few intelligent natives who are cultivating this branch of botany, but China is still an unknown land, and the accessions to our knowledge of British India, in its broadest sense, are but few and far between. The islands are still

almost in the same position as they were. The southern hemisphere exhibits some improvement, but this is principally around old centres. In South America activity has been confined chiefly to the eastern side, south of 20°, and for about twenty degrees southward, but beyond that all is silence. The hopes that the Dark Continent, which has evinced so much vitality in other directions, would furnish good botanical records have not been fulfilled, and even the temporary activity at the Cape has subsided into stagnation. From our point of view the whole of Africa is nearly as it was in 1874. The colonies of Australia have, nevertheless, added much to our knowledge, through the efforts of a few local botanists, and acquired the distinction of possessing a combined Flora of their own, for the Fungi of five of the colonies. Other islands of the Pacific are much as they were, and for the rest of the world we can recognise no alteration, except perhaps some additions to our knowledge of parts of Northern Asia, and a little more of Egypt.

Even in our own country we are conscious that Fungi are more erratic in their appearance and disappearance than flowering plants, and even than other cryptogams. It is in the experience of every one that a species, or even an entire genus, which is common in one year becomes scarce in the next; or that a comparatively common species may gradually become rare in certain localities, through a series of years, and at length vanish altogether. General conditions of temperature, or humidity, affect the appearance of fleshy Fungi much more than it does that of any other plants, and sometimes it is impossible to account for the fluctuation. For instance, in 1893 there were generally more of the common mushroom to be found in England than in any period during the previous thirty years, and yet all other Agarics were remarkably scarce.

The fleshy Hymenomycetal Fungi, of which the mushroom is the type, belong almost exclusively to temperate regions; as warmer countries are approached, they are only found at high elevations, whilst their representatives near the sea level belong to genera in which the substance is tough and leathery, and the proportion of water in their composition is comparatively small. Hence we find that nearly all the Fungi of the

Agaric type to be met with constantly in the tropics belong to such genera as *Marasmius*, *Schizophyllum*, *Lentinus*, and the almost woody *Lenzites*. As we approach the cold polar regions, fleshy Fungi gradually disappear in the face of frost and snow.

If we accept the number of gill-bearing Fungi as 5200 species, we shall find that those genera in which they are tough and elastic, rather than brittle and fleshy, contain about 800 of that number, and all of these have white spores. So that not more than one-seventh of the total number of gillbearing Fungi can be regarded, generally, as capable of supporting a tropical climate. Then, again, of this number of 800 a certain proportion will be found in temperate regions, not less than 320 of this total being recorded, so as to leave only 480 as exclusively tropical or subtropical amongst the Tenaces genera of Agaricini. But to these must be added 550 whitespored species, of the fleshy kind, that have at some time or other been recorded for some tropical locality, including all those which may have been found at a great elevation, and consequently in a temperate region; and, finally, 450 species with coloured spores; making a total of 1480 species which have been found in tropical or subtropical countries. It must, however, be remembered that of these 1000 species of Agarics, of the more fleshy kind, which have been found in the tropics, a great many of them are really species which belong to a temperate zone, and it would be difficult to estimate how many of them have been found only at a considerable elevation, as on the slopes of the Himalayas and the Andes: Whilst a proportionately large number of species of Lepiota have been found in warm countries, as in Ceylon, it is remarkable that of Cortinarius, Russula, and Lactarius, which number some 626 species, only 12 have been met with in tropical regions.

It may fairly be estimated that not less than 4000, but possibly more, species of *Agaricini* have been recorded in temperate climates. By far the largest number of these belong, either exclusively or conjointly, to Europe and North America. Of these 2800 belong to Europe, many of them extending into the United States, whilst 505 are found in the United States which do not occur in Europe, which leaves only

700 species to be distributed over all other temperate regions of the world. Thus we arrive at the conclusion that not more than one-tenth of known species of Agaricini are tropical, whilst from circumstances of locality, elevation, etc., as many as three-tenths have occurred in tropical countries; that more than half of the total number of Agaricini occur in Europe, and nearly two-thirds in Europe and North America. Therefore the northern temperate zone is the most favourable for the Agaricini, and there is no reason to doubt that the temperate regions of Asia will nearly equal those of Europe and America when they are properly explored.

If we take two genera which systematically follow each other, Amanita and Lepiota, we shall find remarkable divergences in their distribution, an explanation of which we discover in the fact that in the former the species are large, soft, and fragile, containing much water, whilst in the latter a great number are small, and all are dry and tough, as compared with other true Agarics. Hence the former genus is essentially that of the temperate, and the latter of the subtropical zone. In Amanita we reckon 80 species, of which 61 are European and North American, and 9 Australian. The four Indian species only occur high up on the Himalayas, and the one South American on the slopes of the Andes. Hence the only tropical species to be accounted for are two in Ceylon, one in Algeria, one in Java, and one in Cuba; the Javanese is doubtless not an Amanita at all. In this case seven-eighths are distinctly located in the temperate zone, one-twentieth at a temperate elevation, and only onetwentieth presumably tropical. On the contrary, in Lepiota, with a total of 225 species, there are 118 belonging to temperate regions, and 107, or nearly one-half, to the tropical. This is a greater proportion than occurs in any other genus of the fleshy Agarics. Those of the temperate zone are 88 for Europe, 16 wholly United States-adding of course a great number of European-and 13 Australasian (out of a total of 33) and 1 Siberian. Those of the tropical zone are-68 for Ceylon, 6 for India, 11 for South Africa, 15 for South America, 3 for Cuba, and 4 for Bonin Island, Java, and Hong-Kong. Circumstances like these render it extremely difficult

to elaborate any scheme of general distribution. In the case of the two genera given above, it should have been stated that both are wholly terrestrial, and similar in their habitats.

The genus *Cortinarius* is one of considerable interest, not only for the beauty of many of the species, but also on account of its distribution. The number of described species is 391, of which 371 belong to Europe and the United States, and of these 68 are confined to America. The residue include 14, chiefly from the most southern part of South America, really temperate, 1 from Tasmania (nine other European species occur in Australia), 3 species from a temperate elevation on the Himalayas, and 1 species each from Japan and the Canaries. The only tropical species is one from Brazil. This is, therefore, a genus of strictly temperate regions, not a single species being found in Ceylon, the West Indies, or Africa. Two hundred of the 371 European species are found in Sweden, and about 180 in Great Britain.

The two closely allied genera, *Lactarius* and *Russula*, belong also to the northern parts of the temperate zone. The 119 species of *Lactarius* include 85 European and 27 North American species, one each from Madeira, Tasmania, temperate Himalayas, and Japan. This leaves only the three Algerian species outside of the temperate zone. For *Russula* 112 species are recorded, which are thus distributed—96 to Europe, 12 to the United States, and 2 to Australia. This leaves only two tropical species—one to Ceylon and one to Venezuela. Australia contains 5 species of Lactarius, of which 4 are European; and 10 species of Russula, of which 8 are European.

The only remaining genus which we purpose to analyse is that of *Coprinus*, in which the pileus is usually very thin, the gills deliquescent, and the spores black. The number of described species is 172, of which 117 are European, and 19 peculiar to the United States. The one species from the Canaries is almost temperate, and also the three Australian species. For tropical regions—12 species for South America, 3 for the West Indies, 3 for Egypt and Mesopotamia, and 9 for Ceylon; 1 for Bonin Island, 1 for Java, and 3 for South Africa. Many of the species are widely distributed, and

are not averse to heat, so long as there is plenty of moisture, yet four-fifths of the species belong to a temperate climate.

The next group in importance is that of the Polyporei, with its 2200 species. This includes some genera which are fleshy, and delight in a temperate climate; but the majority are of a leathery or woody substance, and can flourish in any climate, but in many cases require a hot one. We may commence by excluding 257 species of Boletus and allied genera which are fleshy, and partake of the character of the fleshy Agarics, for their love of a temperate region. The old genus Polyporus now constitutes four genera, of which Polyporus is retained as the name of one genus, and includes the annual species, which are at first soft, and prefer a temperate or warm temperate climate. Of the 403 species, 210 are European or North American, but chiefly in the southern parts, whilst more than half the remainder enter the subtropical region. The genus Fomes includes the hard woody species, which are nominally tropical or subtropical, although a few will inhabit temperate countries. One species, Fomes lucidus, is one of the most cosmopolitan of Fungi, and is found all over the world, except in the Arctic zone. Several other species have a very wide range. The remaining genera, such as Polystictus, Trametes, Daedalea, Hexagona, etc., extend through similar countries to the equator, and together constitute the bulk of the tropical Hymenomycetes.

Very little more needs to be said respecting the Hymenomycetes, since the remaining 2000 species follow the same law of distribution, the fleshy to the temperate, the leathery and woody to the subtropical and tropical regions. We remarked of this, a quarter of a century ago, that when the majority of the species of a genus are of a fleshy consistence, it may generally be concluded that it belongs to a northern region, even if it should have some representatives in lands which enjoy more sunshine. Thus the species of *Hydnum* are the principal ornaments of northern forests, where they attain so luxuriant a growth and beauty that every other country must yield the palm to Sweden in respect to them. In *Irpex* and *Radulum* the texture is more coriaceous, and hence we find the species more commonly inhabiting warmer

The Thelephorei have a very wide range, and some climates. species of Stereum are almost cosmopolitan, or are represented by very close allies, whilst Corticium affects generally a more Allied genera are distributed in contemperate region. formity with their texture. The Clavariei are all more or less fleshy, and have their home in temperate regions, being represented in the tropics by Lachnocladium, which is of a dry and leathery texture. Of the total of 240 species of Clavaria there are 146 indigenous to Europe and the United States, and 20 others to a temperate climate, whilst probably 10 of the original number of species belong to Lachnocladium or Calocera, which would account for three-fourths as inhabitants of the temperate zone, and only one-fourth to be accounted for in warmer countries. Of the Tremellini only some of the Hirneolae belong to a subtropical climate.

The Gastromycetes, or puff-ball family, is a comparatively small one, with about 720 species, and these are subdivided into four distinct sections. The Phalloideae are fleshly fetid Fungi, which prefer a warm climate, although a few species reach the south temperate zone. There are only about 93 species, of which 50 at least are tropical. The Nidulariaceae are small, tough species, widely distributed, and of the 65 species about one-third of them are subtropical. The chief section, the Lycoperdaceae, contains about 480 species, of which rather more than one-third belong to Europe and North Australia is the richest country in the world for America. these Fungi, possessing not less than one-fourth of the total number of described species, whilst Great Britain has only about one-sixth. About one-fourth of the whole are tropical The subterranean family, the Hypogaei, is or subtropical. only a small one, containing about 85 species, but there is hardly a record of a subtropical species, and 68 are recorded for Europe, so that it is almost a European family, for hitherto it is not well represented in the United States. From the above we may conclude, in general terms, that the Phalloidei are subtropical; that the Nidulariaceae are generally distributed; that the Lycoperdaceae prefer a warm temperate climate, especially when dry and sandy; and that the Hypogaei are absolutely of a temperate zone, and chiefly European.

The following are recent estimates of the number of Gastromycetes in the countries of Western Europe :- Britain, 78; France, 85; Belgium, 31; Netherlands, 39; Scandinavia, Also in the middle and south-Germany, 75; Italy, 80; 50. and Austro-Hungary, 40. The Hypodermei follow mostly the distribution of the host-plants, as they are all parasitical, and the greater portion inhabit a temperate zone. Estimating the Uredines at about 1430 species, their chief home is in Europe and North America, but follow their host-plants, when those are cultivated, wherever they go. Of these, about 370 are exclusively subtropical, or nearly one-fourth of the whole; the residue may be assumed to belong to the temperate or warm temperate zone. The Ustilagines, about 330 species, have a similar distribution. Bunt, Tilletia caries, and smut, Ustilago segetum, have followed the wheat and oat plant to Australia, as well as has Puccinia graminis, and in some cases cause more mischief than in their original home.

We pass now to the Ascomycetes, of which the principal features of structure have already been given, but we do not intend to attempt any elaborate account of their distribution. The really fleshy species are for the most part in the Discomycetes, and we may repeat that the fleshy species, such as Morchella, Helvella, and the old genus Peziza, are exclusively, or nearly so, inhabitants of temperate regions. The species of Morchella found in the north of India are from temperate elevations, and always of small size. The Trichoscyphae are almost the only Pezizae of hot climates, and they are of a peculiar tough substance. The finest species of fleshy Pezizae are to be found in the North of Europe and America. The tree-morels, or Cyttariae, are confined to the temperate zone of the southern hemisphere. Out of a total of 3800 species, about two-thirds are soft and fleshy; whilst the residue are fleshy when moist, or have a fleshy disc. If we accept Ceylon as an example of a tropical climate, we shall discover that with its 700 species of Hymenomycetal Fungi, the same list contains but 50 Discomycetes. If we separate the strictly fleshy species of Cyttariaceae, Helvellaceae, Pezizaceae, and Ascobolaceae from the rest, we shall have 2390 species, of which no less than 2076 are to be found in Europe and

the United States. Of the remaining 314 the majority will be found inhabiting the temperate zone of the southern hemisphere. Hence this portion of the Discomycetes must be accepted as confined in a remarkable manner to a temperate climate.

The whole of the Pyrenomycetes, according to the latest enumeration, are not less than 10,478, and of these a large proportion belong to Europe and North America,-probably not so much on account of their actual preponderance in nature, as because of the greater attention which has been paid to their collection and investigation. The distribution is rather unequal in such a large group, some large genera being almost tropical, while others are nearly wholly temperate. For example, the Hypocreaceae are fleshy, and hence a large proportion occur in temperate regions. The Dothideaceae and Microthyriaceae, on the other hand, are tropical, or subtropical, and so also are some genera of the Sphaeriaceae. This will appear more clearly if we divide the whole into subsidiary groups, and first examine into the Perisporiaceae, with about 770 species. These again consist of the Erysipheae and the Perisporieae, the latter subtropical, the former The few species of Erysipheae not found in temperate. Europe or North America will be found in temperate Asia or in the temperate zone of the south hemisphere. With the other group it is the reverse, for the European species of Perisporieae are few, and in some genera none, whereas in North America they are found in the southern states. Meliola is really the tropical, or subtropical, analogue of Erysiphe, and with Asterina, Dimerosporium, and Capnodium rarely found, and only in a depraved state in Southern Europe.

The *Hypocreaceae* number nearly 900 species, and these preponderate in temperate regions, but some species extend into the subtropical. The remarkable genus *Cordyceps*, the species of which possess a fleshy stroma, growing mostly on dead insects, has some 50 species, of which 14 are European, 8 North American, 5 Australian—or 27 temperate against 23 subtropical. Again in *Hypomyces*, with 54 species, all except six are found in Europe or North America. And also in *Hypocrea* there are 102 species for Europe and North America, against 54 for all other localities. This will be sufficient to show that the majority are in favour of a temperate climate.

Taking the *Dothideaceae* and *Microthyriaceae* together, the number of species would be about 650. A large number of the species appear as shining black dots or patches on living or fading leaves, and especially the leaves of forest trees. Some, of course, are erumpent on twigs. We have only been able to trace 116 European species, or about one-sixth of the whole, and there are certainly not so many more in the United States, so that two-thirds of the total number will be tropical or subtropical.

Of the 7500 species of the Sphaeriaceae we cannot attempt an analysis. Ellis gives 1680 North American species, which is two-ninths of the whole, and many of these are European also. Some of the species are cosmopolitan, such as Daldinia concentrica; and some, such as Xylaria polymorpha and Xylaria hypoxylon, are found almost everywhere, even in the tropics. Xylaria and Hypoxylon have their representatives all over the world, amid heat or cold, but with an evident preference for the former. In Cuba we find 20 species of Xylaria and 30 of Hypoxylon, in Ceylon nearly the same number of both; but of the simple scattered Sphaeriaceae the number of species is very small,-probably only a very few collectors would observe them or hunt for them, and they require looking after,-yet there is no reason why they should not be as common in the north of Africa or South America as in the United States or the south of Europe. The 300 species of Lophiostomaceae might practically be united with the above, as they follow the same distribution. Of these 170 are European, and only about 20 subtropical. Another small group consists of the Hysteriaceae, in which the texture is that of Sphaeriaceae, but with the habit and compact disc of the Discomycetes. The number of species is also about 300, and some of these are widely distributed; they are capable of bearing a subtropical climate, although only about 84 occur outside of Europe and North America, and not more than half of these are subtropical.

The home of the *Tuberaceae* is in the south of Europe, and of the 145 species 138 are European. The *Phycomycetes*, which include the Mucors; the aquatic moulds (the *Saprolegniaceae*); the *Peronosporeae*, which are plant parasites; the *Entomophthoreae*, insect parasites; and a few small groups, are chiefly European or North American.

Of imperfect Fungi, the Sphaeropsideae almost follow the distribution of the Sphaeriaceae; and the moulds, or Hyphomycetes, prefer a warm damp atmosphere in the warm temperate zone to a hotter region. The Dematiaei reach farther towards the equator than the Mucedines. About 30 species are recorded for Cuba and 50 for Ceylon, and of these the Mucedines are of a low type; hence the 4800 species recorded must be sought in temperate regions.

The yeast Fungi and Microbes, or Saccharomycetes and Schizomycetes, depend so much upon their surroundings that no scheme of geographical distribution can be propounded. The Myxomycetes are much the strongest in Europe and America, and with a few exceptions are almost entirely confined to those regions. A few of the widely diffused species, such as Stemonitis fusca, Physarum cinereum, and Spumaria alba, sometimes appear at remote places, but they seem to be more scarce than would be anticipated in subtropical localities. Although Thwaites found some 50 species in Ceylon, and 30 species were collected in Cuba, they are rarely to be met with in tropical collections. Out of a total of 450 described species, we can only find 67 that are not represented in Europe or North America.

This appears to be the most complete general survey which we can arrive at with our present knowledge of the Fungi of tropical and subtropical regions, in which the information is most fragmentary. In many cases our knowledge of the Fungi of any given country depends on the work of a single collector, and in no single instance has a tropical country been thoroughly investigated. For the larger, woody, or otherwise persistent species there is no difficulty, as they are conspicuous objects, readily seen, easily collected, and can be conveyed without much difficulty; but the fleshy species, which soon decay or deliquesce, and the minute species, only to be seen with a

lens, never find their way to the places where they could be identified and recorded. Hence the advantages which the Mosses, the Lichens, and even the Algae possess are denied to the Fungi, so that the complete history of their distribution can never be written.¹

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¹ See also M. E. P. Fries, "Observations on the Geographical Distribution of Fungi," in the Annals of Natural History, 3rd series, vol. iv.

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CHAPTER XXVIII

APPENDIX ON COLLECTING

IT will be manifest from the foregoing chapters that the importance of obtaining mature and perfect specimens for examination and determination cannot be too highly estimated. It is not only essential for the determination of any species, but in many cases even the genus, that fructification should be present. In classification nearly everything depends upon the spore, and if no spores are present, and only the vegetative system is developed, any identification is the merest chance. The true relations of an Agaric can only be sought after the colour of the spores has been determined. This is readily done by cutting off the stipes, and inverting the pileus with the gills downwards upon a piece of paper, and allowing it to remain all night in that position. In the morning the spores, if mature, will have fallen upon the paper, in radiating lines, corresponding to the gills. If it is suspected that the spores are white, it is preferable to invert the pileus on a piece of black paper, but, if they are presumed to be coloured, then white paper will suffice. When the colour of the spores has been determined, it can be seen to which of the primary groups the species must be referred, whether Leucosporae, Rhodosporae, or any other. This method may be resorted to with all the Hymenomycetes with advantage, although it is nowhere so important as with the Agaricini.

The value of the spores in classification is not confined to the Hymenomycetes, but pervades the whole of the Fungi. Those minute species in which the fructification is enclosed in a perithecium, having the habit of a Sphaeria, must, in the first instance, exhibit fruit before it can be affirmed whether, by

virtue of the presence of asci, it should have its place in the Pyrenomycetes, or whether, on account of their absence, it must be relegated to the Sphaeropsideae. External appearance will furnish no direct evidence as to its place in the system, and hence a knowledge of the spores is again the first step in identification, without which it is impossible to proceed.

The moulds, or Hyphomycetes, again, when devoid of conidia, are no better than a condition of mycelium. A mass of sterile hyphae is only equivalent to mycelium, even though some of the branches may be erect, as if they exhibited the intention of producing gonidia. When the gonidia are present upon the branches, then the fertile threads possess a new importance, as they become gonidiophores, and in connection with the gonidia determination of the species is probable.

Spotted leaves are often collected by the inexperienced on the assumption that, whenever a living leaf has become spotted in a particular manner, the spotting is due to the presence of a Fungus. In many instances the assumption will prove to be correct, but even then it will not be sufficient to know that mycelium, or even small perithecia, are present, if no mature fruit can be found. Many a weary hour of fruitless labour may be expended in the examination of spotted leaves which do not furnish the organs essential to an accurate diagnosis.

Hence it will be evident that the collector, even if he aspires to be nothing more, must acquire sufficient elementary information to guide him, and prevent the accumulation of a store of waste material, in which a pocket lens will give no evidence of Fungus growth in the condition of fructification. A little knowledge and experience may be sufficient to determine whether a Hymenomycete is mature, or whether there is any ground for the belief that in other cases reproductive organs are present, in some form or other, whilst a larger experience and a more extended knowledge may be necessary for an accurate determination.

When it has been ascertained that a Fungus has all the appearance of possessing mature fructification, the question is sure to arise as to the best method of preserving it for future examination, although it may be premised that fleshy Fungi

APPENDIX ON COLLECTING

can never be examined so satisfactorily as in the fresh state. Wherever it is impossible at once to examine and determine the name of any given Fungus, some effort must be made for its preservation. With the soft and fleshy Agarics no amount of careful desiccation will be satisfactory alone, as they will soon shrink out of all recognition, change colour, and become liable not only to decay, but also to quick destruction by insects. Some persons have suggested the immersion of the fresh specimen in some preserving fluid, such as Goadsby's solution, methylated spirit, glycerine, etc., but none of these can be employed, because the colour of the Agaric will be destroyed, and, worse than all, the spores will be washed away from their sporophores and disseminated through the fluid, suffering decoloration in the process.

The only method which we are prepared to recommend for Fungi of this kind is to make a sketch, or drawing, of the Agaric, with the form, size, and colour as in life. It is not absolutely essential that they should be coloured, although that is best, but the colours should always be stated explicitly upon the drawings. To assist those who are not facile with the pencil, it is recommended that the specimen collected should be divided longitudinally through the cap, and down the centre of the stem. When this is done, one half should be laid on a sheet of white paper, with the cut surface downwards, and the outline traced carefully upon the paper with a sharp-pointed pencil. On removing the specimen there will be left upon the paper an outline of the form of the Agaric, natural size. This may be completed by hand, drawing in the line marking the margin of the pileus, indications of scales (if any exist), the character of the ring (if present), and the scales, lines, or markings of the stem. Another copy of the section, made side by side on the same paper, would give the outline of the gills, and by a little care and practice it would be found easy to draw the line from the stem to the edge of the cap, indicating the point of junction of the gills with the flesh of the cap. This should be done very carefully and accurately, as it must be depended upon to show whether the gills are quite free from the stem at their inner extremity, or whether they are adnexed, or whether they are decurrent, and to what extent they run

347

down the stem. Then, also, it should be shown if the stem is solid or hollow. A little colouring, even if not artistic, would be more useful than mere description of general appearance. Of no less importance is the addition of notes, giving such particulars as cannot be conveyed by the sketch, and these would embrace a statement of habitat, whether growing on the ground or on wood. Amongst other details it should be stated whether the pileus was dry or moist and glutinous, whether the odour was agreeable or fetid or indistinct, whether the taste was mild or acrid and pungent, and whether the gills exhibited any tendency to deliquesce. Finally, if the drawing was not coloured, then the colour of the pileus and stem must be indicated as explicitly as possible, and not vaguely, as red, brown, or gray, but what particular tone of each colour, whether bright red or dull red, dark red or light red, vermilion or crimson, and so on, with any other colour, so that at any time the sketch might be completed in colour and made to represent the species.

Having done this, the next step would be to utilise the specimen itself, supposing it to be an Agaric, by cutting a thin slice from the section of the pileus and stem, laying it upon blotting-paper to dry; the half stem may then be removed and laid to dry, in order to represent the outer surface of the stem; and then the gills and flesh of the half pileus may be cut away so as only to leave a little of the flesh adhering to the cap. By this means we should have three pieces to represent the half Agaric, viz. the section of the pileus and stem, the half stem, and the half pileus, in order to show its external surface. When this is done, the three pieces are to be placed on blottingpaper, covered by one or two thicknesses of paper, and submitted to a gentle pressure, so as to prevent curling, and allowed to dry. At first the papers must be changed every two or three hours, because of the moisture they will absorb, but later on less frequently, until the specimens are quite dry. It will soon become manifest that all trace of the original colour will disappear, and the fragments shrink from loss of moisture; so that, without the precaution of making a previous drawing, there would be little chance of identification. The above suggestions as to drying apply only to species of a compara-

APPENDIX ON COLLECTING

tively large size. There will be hundreds of species so small that they cannot be manipulated further than by taking a section through the cap and stem, after which the specimens will dry up readily in their entirety, and may be kept in small envelopes attached to the drawing. It may be asked, Of what use are these dried fragments, if they are insufficient to determine the species? Granted, that they are only accessories to the sketches, yet they will be sufficient to indicate clearly the colour, size, and shape of the spores, the mode of attachment of the gills to the stem, and the nature of the scales, warts, or silkiness of the surface of the pileus ; but beyond this they can teach very little, nor by any other method yet devised can fleshy Fungi be preserved, so as to retain the form, colour, and size of their natural condition. In a few genera of the Agaricini, such as Lentinus, Lenzites, Schizophyllum, and even Marasmius, where the substance is dry and tough, the species will be readily dried in their entirety, and by aid of a few brief notes may be determined without difficulty. Fleshy species of Boletus and Hydnum will have to be subjected to the above-named process of drawing and desiccation.

The large woody Fomes, and the smaller leathery Polystictus, with the resupinate Poriae and nearly all the Thelephorei, require only to be dried in the air, in some cases under pressure to keep them flat, and in this condition they do not lose much either in colour or form. These are, consequently, the most commonly selected species which are collected by travellers in foreign countries, whilst the smaller or more fragile are neglected.

The whole of the Gastromycetes, excepting the Phalloidei, require little or no preparation. They only need be collected when mature, and dried in the air. The same may be said of the Myxomycetes, which only require to be placed in small pill-boxes, and secured by pins or otherwise, as insects are secured, so as to prevent injury in transit. In no case should more than one species be placed in a single box, or the spores will be transferred and confusion result.

As to the collection of moulds and mucors little can be said, as it seems scarcely possible to carry such delicate objects, even for short distances, without injury. For home purposes we have used small boxes, with fragments of cork glued to the

bottom. It is possible sometimes to obtain some mould upon its matrix, which can be placed in such a box, and pinned to the cork, and thus the conidiophores will remain intact; but the conidia are attached so slightly that very few of them will be found *in situ*. Compact species of such families as Tuberculariae and Stilbaceae are easily transported and preserved.

Parasitical species such as the Uredines and all leaf Fungi are the easiest to collect and preserve, and for them no instructions are required except, perhaps, the suggestion that the leaves should be pressed and dried *flat* in all cases, as they consequently will occupy much less room, and can be examined more readily when dry.

The Discomycetes, although some of them are large and fleshy, such as Morels and the more imposing Pezizeae, may be dried in the air, taking care to note always the colour of the disc when fresh. After being dried they will resume their old form and dimensions when placed in water, although they will never regain the lost colour. The only disadvantage which results from reviving them in this way is, that when they dry again they are liable to become hard, horny, and brittle, except in the tough and leathery species.

It is only necessary now to allude to the largest and most widely distributed group of Fungi, containing not less than 17,000 species. These are the Pyrenomycetes, with the Sphaeropsideae, which latter resemble the Pyrenomycetes in form and habit, but differ in not producing ascospores. These Fungi are to be found on dead wood, branches, twigs, leaves, herbaceous stems, dung, and almost every kind of vegetable debris, the smaller species like little black dots, no larger than a small pin's head, but the largest compound species reaching the size of a man's fist. All of these suffer nothing in the process of drying, and may be as readily determined in five or ten years as on the day in which they were collected. It will be necessary to note the locality and date, and then each specimen can be folded in paper and put away to await a more convenient season. It would be an advantage, when this season arrives, that in every instance, where possible, the name of the host should be indicated-as, for instance, oak, beech, or elm stump, maple branch, or dead

stem of Angelica, Rumex, or other herbaceous plant. For the minute species the pocket lens will consequently be in requisition, but minute and exhaustive research amongst dead vegetable matter, in damp situations, is almost certain to be well rewarded.

We have possibly passed over, in this brief generalisation, small and interesting subsidiary groups, which are technically included under the larger ones, to which attention might have been profitably directed. If we were to advise a young collector as to the course he should pursue with the greatest profit and interest to himself, it would be, that, after making himself generally acquainted with the characteristics of the primary groups, as we have indicated them, he should select for himself a compact family of moderate size, and devote himself to that group alone until he is familiar with all the details; after this course of practical education, he might with advantage widen his field of operation and extend his patronage to other groups. By concentration of his thoughts and energies he will be the better able to cope with the difficulties, and master the details, of a comparatively small group, than by attacking a large one. There are several of such groups available-as, for instance, the Uredines, the Ustilagines, the Myxomycetes, the Gastromycetes, or even the Hyphomycetes. In whatever direction his inclination may lead him, the student will find peculiarities, and adaptations of methods of examination and study, applicable to the special objects of his research. In none will he be able to proceed far without the use of the microscope, and we would strongly urge upon him the necessity of cultivating the power of the hand in making sketches and drawings, either with or without the use of the camera lucida, or some form of substitute. Accurate drawings, made to scale, of reproductive bodies, structural details, modes of development, and other minutiae will always prove a source of satisfaction in the future, and a help towards progress.

Finally, we would urge also upon the young and inexperienced never to rest content with being mere collectors, since the knowledge so obtained is liable to become superficial and empirical; but, on the contrary, to examine for

himself, as thoroughly and completely as possible, every organism which he acquires in his own selected group, and endeavour to ascertain all that is possible of its life-history. The whole history of one species, worked out with perseverance and intelligence, will present the key to a knowledge of many kindred species, and always prove to be a valuable contribution to science, when the names of species are changed or forgotten.

GLOSSARY

ACROGENOUS-produced at the summit.

- Acrogonidium-gonidium at the summit of a gonidiophore.
- Acrospore-spore formed at the summit of a sporophore.
- Accidiospore spores formed in an Aecidium, serially and successively abstricted.
- Aecidium cup shaped receptacle in the Uredines, enclosing a hymenium producing Aecidiospores.
- Aethalium body formed in Myxomycetes from a large combination of plasmodia.

- Alveolate-pitted like honeycomb. Amoeboid-like an Amoeba; applied to a protoplasmic body which creeps by putting out and retracting pseudopodia.
- Angiocarpous-having the hymenium developed within the sporophore, and covered from the first by a special envelope.
- Annulus-in Hymenomycetes, portion of the veil, or tissue of the stipe forming a collar or ring.

Antheridium-male sexual organ.

- Archicarp-cell, or group of cells, fertilised by a sexual act.
- Arthrosporous-such Schizomycetes as have no endogenous spore-formation.

Asciferous, Ascigerous-bearing asci.

- Ascocarp-a sporocarp bearing asci and sporidia, or ascospores.
- Ascogenous-producing asci.
- Ascophore sporophore bearing an ascus.
- Ascospore-spore contained in an ascus =sporidium.
- Ascus, Theca-large cell or sac in which ascospores are developed, typically eight.
- Autoecious, or Autoxenous-a parasite which goes through the whole course of its development on a single host. Autonomous-plants that are perfect

and complete in themselves, not forming part of a cycle.

- BASIDIOPHORE-sporophore bearing a basidium.
- Basidiospore-spore produced at the apex of a basidium.
- Basidium-mother cell from which spores are abjointed. In Hymenomycetes, a sporophore bearing from one to four spores on short sterigmata.
- Brood-cell-same as gonidium or conidium.

CAP - in Hymenomycetes, same as pileus.

- Capillitium-sterile threads or tubes, often branched, mixed with the spores in the spore-masses of some Gastromycetes and Myxomycetes.
- Carpophore-generally, the support of the fructification ; specially, the stalk of a sporocarp.
- Carpospore-spore formed in a sporocarp.
- Chlamydospore-spore with a very thick spore-membrane.
- Chlorophyll the green colouring matter in plants, absent in all Fungi.
- Clamp-connection small semicircular protuberance attached through its length, or leaving an eyehole, to the walls of two adjoining cells of a septate hypha, and stretching over the septa between them, communicating with one or both, or cut off from both, and forming a clamp-cell.
- Cleistocarp-ascocarp forming a completely closed cavity, which is finally ruptured to permit the ascospores to escape.
- Columella-sterile central body in a sporangium.
- Concatenate linked together in a chain.

Conceptacle—a superficial cavity opening outwards within which conidia or sporules are produced.

Conidiophore—same as gonidiophore. Conidium—same as gonidium or broodcell.

- Cortina, or curtain—in Hymenomycetes, marginal veil, ruptured from the stipe and hanging from the edge of the pileus, or around the stipe in threads.
- Cryptogamia applied to the lower orders of plants in which there are no conspicuous flowers, as there are in the Phanerogamia.
- Cuticle, or pellicle—the separable outer layer.
- Cyst—a bladder specially applied to the terminal sporangia of Mucors.
- *Cystidium*—in Hymenomycetes, large projecting cells of the hymenium, extending beyond the basidia and paraphyses.
- DICHOTOMY-branching in pairs in a forked manner.

Disc—the hymenium of a discocarp.

- Discocarp—an open ascocarp in which the hymenium is exposed whilst the asci mature.
- *ELATER* in Myxomycetes, a free capillitium thread, mostly spirally marked or warted.
- Endogonidium—gonidium formed within a receptacle.
- Endophytal—growing within another plant.
- Endosporium, Endospore innermost coat of a spore.
- Entomogenous-growing upon or within insects.
- Epiphytal growing upon another plant.
- Episporium, Epispore outer coat of spore.
- *Excipulum*—outer envelope of a discocarp developed as part of the receptacle.
- FACULTATIVE PARASITE—an organism which normally goes through its whole course as a saprophyte, but which may also go through its course either wholly or in part as a parasite.
- Facultative saprophyte an organism which normally goes through its whole course as a parasite, but which can vegetate at certain stages as a saprophyte.

- Flagellum whip-like process of a swarm - spore, a single or solitary long cilium.
- Funiculus—in Nidulariaceae, the cord of hyphae attaching a peridiolum to the inner wall of the peridium.
- GAMETE sexual protoplasmic body, which on conjugation with another gamete gives rise to a body called a zygote or zygospore.
- Germ-cell-first product of commencing germination of a spore.
- Gleba chambered spore producing tissue within a sporophore. As in Gastromycetes.
- Gonidiophore sporophore bearing a gonidium.
- Gonidium = conidium, or brood-cell propagative cell, produced asexually, separating from the parent and capable of direct development into a new individual.
- Gonoplasm—portion of protoplasm of antheridium in Peronosporeae which passes through fertilisation tube and coalesces with the oosphere.
- Gonosphere-the same as oosphere.
- Gymnocarpous—having the hymenium exposed while the spores are growing.
- HABITAT-the place in which a plant grows.
- Haustorium—special branch of filamentous mycelium which serves as an organ of adhesion and suction.
- Heteroecious—forms which pass through separate sections of their complete history on different hosts.
- Heterosporous-having spores asexually produced, of more than one kind.
- Homosporous, Isosporous-having spores asexually produced, of only one kind.
- Hymenium—spore mother-cells, aggregated in a continuous layer upon a sporophore, or that specialised portion termed the receptacle.
- Hymenophore-portion of a sporophore which bears a hymenium.
- Hypha, as applied to Fungi—a cylindrical, thread-like, simple, or branched body, consisting of a tubular membrane enclosing protoplasm, growing apically, and often becoming transversely septate.
- versely septate. Hyphal bodics—irregular bodies analogous to mycelium in Entomophthoraceae.
- Hypothecium-layer of hyphal tissue immédiately beneath a hymenium.

INTRALAMELLAR TISSUE - same as trama in Hymenomycetes.

Isogamy—conjunction of two gametes of similar form.

Isosporous—same as Homosporous.

LACTIFEROUS, LATICIFEROUS—bearing or conveying latex, or milky fluid.

- Lamella—in Hymenomycetes, the gills or folds of the hymenium, radiating from a definite point.
- Lipoxenous applied to a parasite which leaves its host and completes its development independently.
- MACROGONIDIUM, MEGALOGONIDIUMlarge gonidium compared with others

produced by the same plant. Merispore—segment of a sporidesm.

Metaecious-same as Heteroecious.

Microcyst-in Myxomycetes, applied to a resting state of swarm-cells.

Microgonidium—small gonidium compared with others in the same species. See Macrogonidium.

Multilocular spore—see Sporidesm.

- Mutualism—symbiosis of two organisms living together and mutually helping and supporting each other.
- Mycelium-vegetative portion of Fungi composed of one or more hyphae.
- NECK, or COLLUM—conical or cylindrical prolongation of the apex of perithecium in Pyrenomycetes.
- OIDIUM a generic term, sometimes applied to concatenate conidia, which are successively abstricted at the apex of hyphae.
- Oogamy-conjugation of two gametes of different form.
- *Oogonium*—female sexual organ, usually a spherical sac containing one or more oospheres.
- *Oosphere*—spherical body which develops the oospore as the result of fertilisation.
- Oospore-product of fertilisation in oosphere.
- Ostiolum—in Pyrenomycetes, orifice or mouth of perithecium, or pyrenocarp through which the spores are discharged.
- PARAPHYSIS—sterile, thread-like hyphal branch accompanying the mother-cells in a hymenium.

Parasite—organism living in or upon, and at the expense of, another. Pathogenous—producing disease.

Penicillate-like a pencil of hairs.

- Peridiolum—little Îenticular bodies in Nidularieae, which are free, or attached by a funiculum to the inner wall of the peridium. Each peridiolum enclosing a mass of spores.
- Peridium—the enveloping coat of a sporophore, or receptacle in which the spores are developed in a closed cavity. In Gastromycetes sometimes called the uterus, the contents being the gleba.
- Perithecium, or Pyrenocarp—ascocarp with the margin incurved so as to form a narrow-mouthed cavity. A more or less globose receptacle, perforated at the apex.
- Pileus—in Hymenomycetes, the conical or dome-shaped cap bearing the hymenium on the under surface. Extended also to other compound sporophores.
- Plasmatoparous in Peronosporeae, when in germination the protoplasm of a gonidium issues as a spherical mass, which becomes invested with a membrane and projects a germ-tube.
- Plasmodium in Myxomycetes, the multinucleate protoplasm, exhibiting amoeboid motion.
- Pleomorphism—when more than one independent form in the life-cycle of a species occurs it is called pleomorphy.
- Pleuroblastic—in Peronosporeae, those forms which produce vesicular lateral outgrowths that serve as haustoria.
- Pore—in Pyrenomycetes it is the ostiolum; in Polyporei the mouth of the tube which encloses the hymenium.
- Promycelium the product of tube germination of a spore which constricts off a number of spores, unlike the mother spore, and then dies.
- the mother spore, and then dies. *Pseudoperidium* — the cup, or receptacle, in Aecidium.
- Pseudopodium—in Myxomycetes, the protruded and retracted protoplasm of amoeboid forms, imparting motion.
- Pycnidium—in Ascomycetes, a cavity resembling a perithecium containing gonidia, which are termed pycnogonidia.
- RECEPTACLE general term for hollowed-out body, containing other bodies.

Resting-spore—a spore which lies dormant or rests for a period before germination. A hibernating spore.

Resting stage, resting period-stage or period of quiescence or dormancy. Resupinate-attached to the matrix by

the back.

Bhizoid, or *Rhizine*—thread-like delicate organs of attachment.

- SAPROPHYTE a plant living and thriving on dead organic matter.
- Sclerotium—hard tuber-like body filled with reserve material, of the nature of a compact mycelium, which remains dormant for a time, and then develops sporophores.
- Scolecite—peculiar rudimentary bodies in Discomycetes which are probably the first distinction of fertile from sterile hypha, doubtfully described as sexual.
- Sorus—a heap, or aggregation, chiefly of reproductive bodies.

Spermatium-male gamete cell which conjugates with a trichogyne.

Spermatozoid—thread-like bodies, possessed of motion, and supposed to be fecundative.

Sporangiole—small sporangium, produced in some genera of Mucors, supplementary to large sporangium.

Sporangiophore—the sperophore of a sporangium.

- Sporangium—envelope or sac in which spores are produced.
- Spore—in a general sense it is a reproductive cell, which becomes free, and is capable of developing into a new plant; in a special sense, restricted to the Hymenomycetes.
- Sporidesm multicellular spore-body, becoming free, of which each cell is an independent spore.
- Sporidiolum—diminutive of sporidium —applied to promycelial spores in the Uredines.
- Sporidium—in Ascomycetes, a spore developed in an ascus. In Uredines a spore abjointed on a promycelium.

Sporiferous—bearing spores. Sporocarp—multicellular body, ·de-

veloped sexually from an archicarp, unlike the body which produced the archicarp, and serving to form spores.

Sporogenous-producing spores.

Sporophore-branch which bears spores, or mother-cells.

Sporule -- designation for spore, en-

closed in a perithecium, in imperfect Fungi, such as Sphaeropsideae, without asci.

- Sterigma, Spicule-slender stalk-like branch of basidium bearing a spore.
- Stipe—general term for the stalk of a sporophore, usually applied to the stem of Agarics.
- Stroma—Fungus body with the form of a cushion, crust, club, or branched expansion; usually supporting compound fructification.
- Stylospore-spore borne on a filament.
- Suspensor-in Mucors; club-shaped or conical portion of hypha, adjoining a gamete cell after its differentiation.2
- Swarm-cell-naked motile protoplasmic body.
- Symbion—an organism living in a state of symbiosis.
- Symbiosis-the living together of dissimilar organisms.
- TELEUTOSPORE—in Uredines, the ultimate spore of the cycle which is capable of germinating and producing a promycelium.
- Thallophytes—cellular Cryptogamia. Includes Algae and Fungi, where there is no differentiation into stem and leaf.
- Thallus the vegetative body of a Thallophyte.

Theca—the same as ascus.

- Thecaspore synonymous with ascospore.
- Trama—in Basidiomycetes, the middle tissue of the gill plates, or other projections of the receptacle which bears the hymenium.
- Trichogyne—female receptive portion of an archicarp to which the spermatia become attached.
- Tubulus, Tube-in Hymenomycetes, the tube lined with the hymenium, as in Polyporei.
- UREDO-hymenium producing uredospores.
- Uredospore Uredogonidium—in Uredineae, spore formed upon a sporophore from which it separates at maturity, and on germination produces a mycelium bearing uredospores or teleutospores, or both.
- Uterus-same as peridium in Gastromycetes.
- VEIL, Velum in Hymenomycetes, special envelope in which the growth

356

of the whole or part of the sporo-phore takes place.

Volva, Velum universale—in Hymeno-mycetes, sac enclosing the whole of a sporophore at first, but ultimately ruptured at the apex by the expanding pileus.

YEAST FUNGUS-species of Saccharomyces.

- ZOOGLAEA—in Schizomycetes, a colony imbedded in a gelatinous stratum. Zoogonidium active gonidium. See
- Zoospore.
- Zoosporangium sporangium contain-

ing zoospores. Zoospore—motile spore. Zygote, Zygospore—spore resulting from the conjugation of two similar gametes.

INDEX

AECIDIUM, 243 Agaric, parts of, 32 Agaricus, section of, 127 Alternation of generations, 70 Anthrax, 295 Appendix on collecting, 345 Archicarps, 229 Arthrospore, 292 Artificial cultures, 249 Asci and paraphyses, 104, 166 Ascomycetes, 164 Ascus and sporidia, 45 Aseptate mycelium, 16 Atrophied basidia, 121

BACTERIA, 291 Basidia, 41, 120 Basidiomycetes, 115, 119 Beech Morels, 186 Bird's-nest Fungus, 153 Black moulds, 278, 283 Bunt spores, 255

CALOSTOMA, development of, 156 Capillitium, 43, 309 Capsular Fungi, 197 Carpophore, 22 Carpophores agglomerated, 28 Census of Fungi, 319 Clamp-connections, 11, 150 Classification, 93 Clavate carpophore, 29 Clinospore, 45 Cluster-cups, 48, 242 Collecting, instructions, 345 Coloration of pileus, 34 Colouring matters, 85 Columella, 36, 313 Compound carpophore, 23 Sphaeriaceae, 213 Conidiophore, 51 Conidium, 45 Coniomycetes, 259 Conjugating Fungi, 227 - hyphae, 62

Conjugation in Peziza, 58 Constituents of Fungi, 84 Crested sporules, 275 Cup-shaped receptacle, 37 Cuticle of pileus, 33 Cystidia, 41, 121 Cyttaria, 186

DEFINITION of Fungi, 1 Dematiaei, 278, 281 Destructiveness, 107 Development in Erysiphe, 55 —— of Eurotium, 56 Diatrype and Valsa, 211 Dichocarpism, 64, 286 Dimorphic Fungi, 64, 286 Discoid Fungi, 172 Discomyeetes, 173 Disintegration by mycelium, 21 Distribution, 317, 324 Dothideaceae, 207 Dust Fungi, 259

FERTILISATION, 53 Fish-moulds, 232 Flies and Fungi, 152 Formation of zygospore, 17, 59 Fructification, 41 Fungi, census of, 319 — and Lichens, 109 — in general, 95 — the Great Destroyer, 109 Fungus poisons, 86 GAPING Fungi, 222 Gastromycetal carpophore, 26 Gastromycetes, 149 Geographical distribution, 324 Germination of zoospores, 76 Gleba, 43 Globose carpophore, 29 Gloeosporium, 272 Glossary, 353 Glycogen in Fungi, 87 Growth of Bacteria, 291

HAPLOPHYLLAE, 132 Hereditary transmission, 81 Heteroecism, 245 Hymenium, 42, 102, 124 — of Peziza, 44 Hymenomycetes, 126 Hypertrophied basidia, 122 Hyphal bodies, 18, 235 Hyphomycetes, 277 Hypocreaceae, 202 Hypodermeae, 78, 242 Hysteriaceae, 222 — analogues, 268

IMPERFECT capsular Fungi, 259 Imperfect Fungi, 103 Introduction, 1

LACTIFEROUS vessels, 25, 33 Lichens and Fungi, 3, 109 Lycoperdáceae, 154

MACROCYSTS, 58 Macronemeae, 280 Melanconieae, 260, 271 Melanconis and conidia, 67 Melasmia and Rhytisma, 65 Mesomycetes, 113 Metuloids, 42, 143 Microbes, 290 Micronemeae, 280 Microthyriaceae, 219 Microzyma, 297 Milky juice, 25, 33, 89 Morels, 178 Moulds and their conidia, 50, 277 Mucedines, 278 Mucor, development, 229 Mucoraceae, 228 Mushroom spawn, 9, 97 Mycelium, 9, 97 Mycomycetes, 113 Mycorhiza, 20 Myxomycetes, 304 Myxomycetes not animal, 19, 304

NAKED hymenium, 41 Naked-spored Fungi, 102, 119 Nidulariaceae, 153

OIDIUM and Uncinula, 66 Old definitions, 96 Oogonia, or female cells, 60 Oogonium and oosphere, 232 Organography, 7 Ostiolum, or mouth, 38

PARACYSTS, 58 Paraphyses, 42, 121, 168 Pathogenous microbes, 296 Perennial mycelium, 20 Peridiola, 46, 153 Peridium, 36 Perisporiaceae, 198 Perithecium, 38, 48, 198 Peronospora, development, 231 — reproduction of, 77 Peronosporaceae, 230 Peziza sclerotia, 15, 180 Phalloideae, 151 Phosphorescence, 89 Phycomycetes, 113, 227 Pileate receptacle, 31 Plasmodia, 305 Podaxis, structure of, 160 Polymorphism, 220 Polyphagus, development, 237^{*} Polyporei, 135 Promycelial spores, 246, 254 Pseudoperidia, 48 Puccinia, life-history, 78 Puff-ball Fungi, 149 Pyrenomycetes, 197

RECEPTACLE, 31 Resin in Polyporei, 88 Rhizomorpha, 12, 99 Root Fungi, 20 Rust Fungi, 242

SACCHAROMYCETES, 290, 298 Saprolegnia, development, 233 Saprolegniaceae, 232 Saprophytes and parasites, 73 Schizomycetes, 290, 293 Schizophyllae, 130 Sclerotium, 14 Scolecite, 46, 57, 175 Section of Agaric, 32 Sessile pilei, 35 Sexuality, 54 — in Achlya, 60 — in Peronospora, 61 — in Peziza, 176 Sexual reproduction, 229, 234 Simple Sphaeriaceae, 214 Slime Fungi, 304

Smut Fungi, 251 Spermatia, 45 Sphaeriaceae, 205 - analogues, 261 Sphaeropsideae, 259 Sporangium, 50 Spore, naked, 45 - division of Agaricus, 130 – forms, 45 – value, 345 Sporidium, 45 Sporule, 45 Stinkhorn Fungi, 151 Stipe, or stem, 25 Stylospore, 45 Stylosporous fructification, 49 Subterranean Fungi, 189 Suspensor and gamete, 229 Swarm-cells, 305

TABLE of groups, 117 Teleutospores, 242 Thallogens, 2 Thallophytes, 3 Tilletia, germination, 63, 255 Touchwood, 99 Trama, 32, 128 Tremelloid Fungi, 145 Truffles, 191 Tuberaceae, 190 Tubercularia and Nectria, 204 Two forms of fruit, 69

UREDINEAE, 242 Ustilagines, 251

VARNISHED pilei, 88 Vegetative system, 11 Vinegar plant, 100

WHITE moulds, 278

XYLARIA and stroma, 206

YEAST Fungi, 298

ZOOSPORES, zoogonidia, 227 Zygomycetes, 229 Zygospore formation, 17, 59 Zygospores, 227

THE END

Printed by R. & R. CLARK, LIMITED, Edinburgh.

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