COMPARATIVE MORPHOLOGY OF FUNGI

BY

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PREFACE TO THE AMERICAN EDITION

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

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

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

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

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

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

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

C. W. Dodge.

Cambridge, Massachusetts,
December 1, 1927.

PREFACE TO THE GERMAN EDITION

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

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

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

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

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

Dr. Ernst Gäumann,
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Docent, Federal Technical High School.

Oerlikon-Zürich,
October, 1925.

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COMPARATIVE MORPHOLOGY OF FUNGI

CHAPTER I

INTRODUCTION

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

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

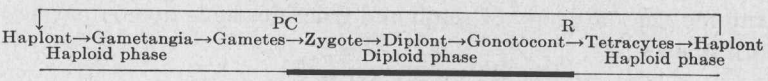

DIAGRAM I.

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

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

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

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

CHAPTER II

THE THALLUS

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

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

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

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

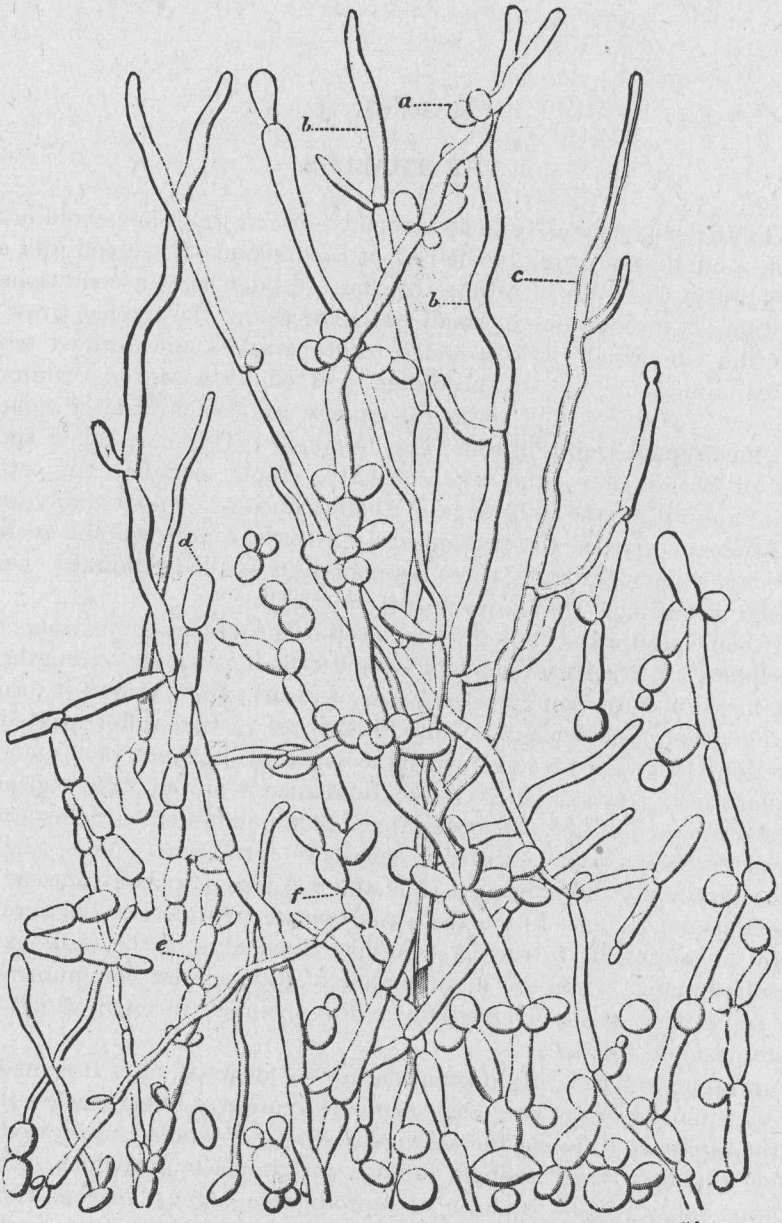

FIG. 1.—*Monilia candida.* Formation of sprout cells. *b*, *c*, typical hyphae; *a*, *e*, *f*, sprout cells; *d*, oidia. (× 1,000; *after Hansen.*)

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

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

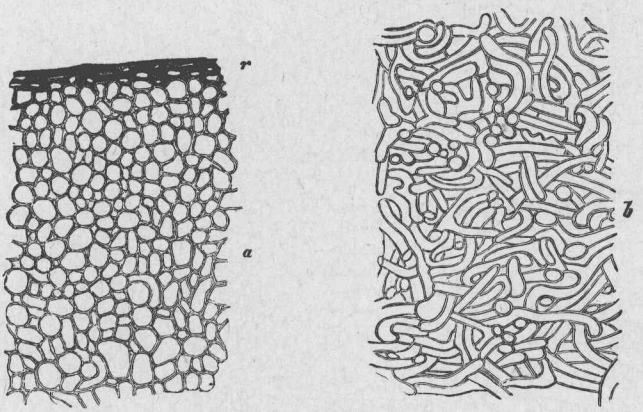

FIG. 2.—*Claviceps purpurea.* Section through a sclerotium. *a*, peripheral layer of pseudoparenchyma; *b*, core tissue of prosenchyma; *r*, rind. (× 360; *after Tavel.*)

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

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

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

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

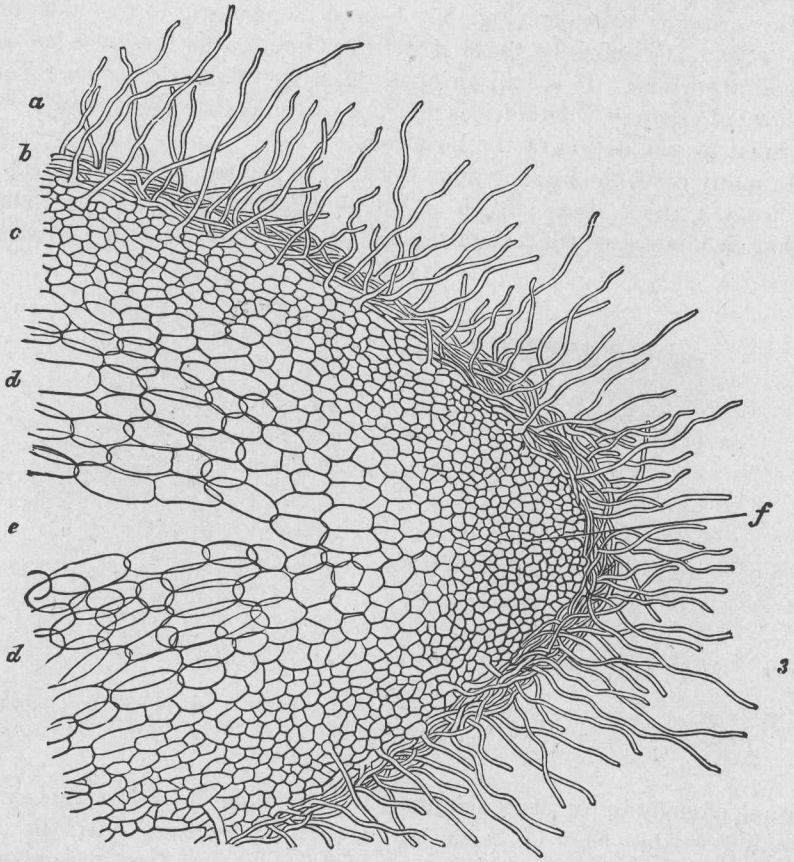

FIG. 3.—*Armillaria mellea.* Longitudinal section of tip of rhizomorph. *a*, loose hyphae; *b*, gelatinous, loosely interwoven hyphal layer; *c*, *d*, core layers; *e*, central cavity; *f*, apical meristem. (× 300; *after Hartig.*)

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

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

CHAPTER III

FRUCTIFICATIONS

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

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

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

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

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

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