FOREWORD

NO class of microörganisms has been more intimately associated with the progress and development of the human race than the yeasts. Since the earliest times, these microörganisms have been used to bring about changes which it would have been difficult to have accomplished by other methods. Since microscopic examinations have revealed the presence of yeast cells in bread found with Egyptian mummies, it is known that these people were familiar with yeast fermentations, although they probably did not have explanations for the changes which were observed. The Norsemen prepared an alcoholic drink from milk, as is done today by certain nomadic races, the fermentation of which was, in part, caused by yeasts. Today we find the yeasts of ever-increasing interest and importance. The food microbiologist must understand the physiology of these organisms if he is to successfully cope with them. They are assuming greater importance in medicine, especially in relation to certain deficiency diseases, constipation, and skin infections. Great industries have been established which rest entirely on the chemical changes brought about by yeasts and their enzymes; some of them would be developed with difficulty, were it necessary to use strictly chemical methods. The compressed yeast industry itself has reached a high state of development with its several factories located in different parts of America and distributing agencies in practically all of the cities and villages. Many industries have been greatly changed by the availability of fresh, active yeast whenever it is needed. Despite the facts that yeasts have always been of great significance to the human race and that they will probably have greater significance in the future, it remained for Guilliermond to collect the various data, which have accumulated in regard to them, into one volume. Several treatises have been prepared which deal with the yeasts in relation to fermentations, but no real definitive treatise on the yeasts, as such, has appeared which is comparable to the volume prepared by Guilliermond. The investigations of this authority make the book especially valuable. These facts made it seem advisable to translate the volume for publication in the English language in order that the data might be available to the practitioners and students who do not read

the French language. It is sincerely hoped, however, that the rendition of this book into the English language will in no way inhibit the study of the French language — that language in which Pasteur, Bernard, Magendie, Berthelot, and others have published their classic investigations.

This English edition is based on Guilliermond's "Les Levures," which was published in 1912, appearing as a volume in the section on Cryptogamic Botany of Encyclopédie Scientifique. This series is edited under the direction of Doctor Toulouse. To merely translate a volume on a subject which is being developed as rapidly as the yeasts would be entirely inadequate. Consequently with the collaboration of Professor Guilliermond, the translator has added much new material which has been published since 1912. Without the assistance of Professor Guilliermond, this could not have been done as completely. The English edition may not, then, be regarded as a mere translation of the last French edition.

The rendition of a text from a foreign language into the English language is beset with difficulties which are most clearly appreciated by those who have performed similar pieces of work. In all cases a literal translation has not been attempted; however, the opinions of the original author have been given as closely as possible. It is trusted that this English edition will make it easier for students to pursue their study of these important microörganisms and for the practitioner to more easily solve the problems with which he has to cope. I owe many thanks to my colleagues, too numerous to mention here, for expression of their advice at various times and for their interest during the progress of the work.

FRED W. TANNER

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URBANA, ILLINOIS
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AUTHOR'S PREFACE

SINCE the celebrated memoir by Pasteur on alcoholic fermentation, the yeasts have never ceased to assume an ever-increasing importance in agriculture and the industries. The classic investigations by Pasteur, followed by those of Hansen, have shown the profit that may result from a methodical study of the various species of yeasts, by a knowledge of the conditions necessary for their development and biochemical characteristics for application to the fermentation industries. No one may overlook the benefits which came to such industries by the use of pure cultures and selected species, and the avoidance of yeasts which caused defects in fermented products. The fermentologists have also benefited greatly by these methods. Finally, the relatively recent investigations have shown the relationship of yeasts to certain diseases in man and animals.

From a purely theoretical point of view the yeasts, on account of the facility with which they allow themselves to be cultivated in artificial media, and by the relatively large size of their cells, are especially favorable objects for experimentation upon which very important investigations of physiology, cytology and sexuality have been made. They have contributed appreciably to the progress of general physiology and biology.

It seemed useful to me to collect into one book all of the knowledge required on the morphology, physiology and taxonomy group of fungi, and to arrange it in such a manner that the data would be available for biologists, practitioners in industrial work, agriculturalists and physicians. That is what I attempted to accomplish in the little volume published in the *Encyclopédie Scientifique* under the editorial supervision of Dr. Toulouse.

Professor Tanner, of the University of Illinois, undertook the translation of this book into the English language in order to render it more accessible to American students and American investigators. This is indeed a great honor to me, one which I did not dream of when I prepared this modest work a few years ago. I am very happy to have this indication of friendship between scientific America and France, a friendship which I hope may become stronger and stronger. One sufficiently understands the significance of a scientific alliance of

two nations which by their individual characteristics supplement each other. France claims such great teachers as Lamarck, Claude Bernard, and Pasteur, true pioneers in the field of biology. By her spirit perhaps, too traditionalistic and suppressed by old administrative machinery, she has not always understood fully the real utility of her universities and given to her scientists the necessary means for carrying on their work. On the other hand, America, with no such rich heritage from the past, has built up modern laboratories with a new spirit and equipped them with the necessary resources. She probably possesses the greatest universities in the world. She lays claim to able investigators and, thanks to her marvelous scientific organization and to her numerous investigators, is sure to gain very rapidly a foremost place in the scientific world. If the American savants have the desire to profit by the discoveries of the French, their elders, France has much to gain by imitating America in her practical ideas, her spirit of organization, her methods of work, and her tremendous activity.

The book which Professor Tanner has undertaken to present to the public cannot be regarded as a simple translation of my work; it is a new edition resulting from intimate collaboration of translator and author. Microbiology is progressing so rapidly that the French edition, now six years old, is no longer abreast with recent acquisitions of the science. It was found necessary to make numerous editions and to modify certain chapters in which Professor Tanner and myself have shared the labor. Professor Tanner, known by his work on the biochemistry of bacteria, has undertaken the revision of the Chapter on Physiology of the Yeasts which was no small task, for since the discovery of zymase by Buchner, the biochemical investigations on yeasts have followed each other without interruption and have become increasingly valuable. As for myself, I have borne the task of revising the Chapters on Morphology, Phylogeny and Description of Species, subjects with which I am more familiar. Professor Tanner had, then, a preponderant part in the translation of this new edition and the book has certainly gained much by the collaboration of a physiologist so well qualified.

ALEXANDRE GUILLIERMOND

LYON, *September* 8, 1919

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THE YEASTS

INTRODUCTION

What are Yeasts?

UNDER the name of yeasts have been generally grouped all microorganisms which, when placed in sugar solutions, decompose them into alcohol and carbon dioxide—cause alcoholic fermentation. Knowledge with regard to the chemical properties of the yeasts has, to a great extent, preceded that with regard to their nature. The old word yeasts (Fr. *levure* = Latin *lever*) which emphasized their chemical properties dates from an epoch when no attention was given to their biological significance or nature. But today the name yeast has taken on a restricted meaning among botanists. In the botanical sense, yeasts are unicellular fungi of biochemical interest, spherical or oval in shape, and which multiply by budding. A yeast, then, is a fungus with special morphology. Be that as it may, the term is not applied to an indefinite group of fungi but to a natural one.

Many fungi, more or less developed, living normally with a mycelium are able to reproduce by budding of their filaments, to form cells which have the shapes of yeasts. These multiply in their turn by budding and retain the form of yeasts for many generations. (Fig. 1.) The basidiospores of certain *Basidiomycetes* (*Calcera viscosa*) and ascospores of certain *Ascomycetes* (*Sphaerulina intermixta Taphria*) give rise to yeasts and it is only after living for a certain time in this form that the yeast cells elongate filaments and produce a mycelium. Among the *Ustilaginales*, the sporidia, which spring from the promycelium, exist also in the shape of yeasts; it is this state in which they develop, and which they constantly retain when cultivated in artificial media. The Mucors, when placed in sugar solutions, are able to dissociate their filaments into round bodies, or buds, in a similar manner as the yeasts. *Dematium pullulans* (Fig. 1), a mold with a well-differentiated mycelium, produces in a regular fashion, by budding of its filaments, numerous yeast conidia; when these are cultivated under certain conditions, they are transformed with difficulty into mycelium. Vegetation with forms like yeasts is, then, rather widespread among the fungi.

Aside from these fungi, in which yeast forms are merely stages of development, there are others which live constantly in the forms of

yeasts. These do not present a true mycelium at any time. They reproduce at times by elongation of their cells, which adhere together, forming structures resembling mycelium; but these never offer the complexity of a typical mycelium. In the category of yeasts belong the alcoholic ferments and all of the fungi more generally known under the name of yeasts.

These yeasts, which are often designated as " true yeasts " in contradistinction to " yeast-like fungi " derived from more highly developed fungi, are not distinguishable in any manner from the latter. The general form and the internal characteristics of the cells are the same in both cases. Physiologically, certain true yeasts differ only from yeast forms of molds by their resistance to anaerobic conditions and exceptional activity of the fermenting function, but very many yeast-like structures, derived from fungi more highly developed, are equally capable of producing alcoholic fermentation, and only differ, from this point of view, from true yeasts by a decreased activity of fermentation. On the other hand, a certain number of true yeasts are totally deprived of the fermenting function. It is understood then, how the early investigators were much confused when it became necessary to characterize the yeasts.

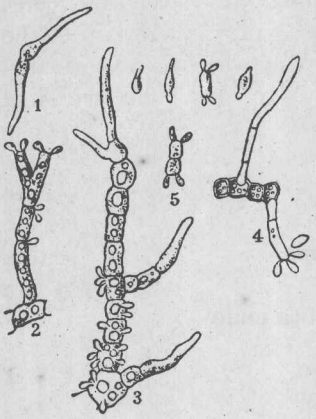

Fig. 1. — *Dematium pullulans.*
1 to 4, Mycelium Forming Yeasts; 5, Yeast-Like Bodies in Process of Budding (after Loew).

In the meantime, an essential difference which did not escape investigators existed between the yeast-like fungi and the yeasts properly so-called. Indeed, most of the true yeasts are distinguished closely from " yeast-forms " by their aptitude to produce resistant endospores at certain stages in their life cycles (unfavorable conditions), in the interior of their cells; the cells are then transformed into sporangia. De Bary, Rees, and Hansen first compared these sporangia to ascs of *Ascomycetes*, considering the true yeasts as autonomous fungi which live only in the form of yeasts and are incapable of developing a mycelium.

This conception is definitely admitted today, as we shall see when the origin and systematic relationships of the yeasts are taken up. The autonomy of the yeasts and their incorporation as a group of *Ascomycetes* have been demonstrated only since Hansen observed their life cycles in nature and since certain investigators have given evidence in the origin of the asc of certain yeasts, of the presence of