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INTRODUCTORY MYCOLOGY

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Fourth Edition

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JOHN WILEY & SONS, INC.
New York Chichester Brisbane Toronto Singapore

ACQUISITIONS EDITOR David Harris
MARKETING MANAGER Rebecca Herschler
PRODUCTION EDITOR Sandra Russell
DESIGNER Lynn Rogan
MANUFACTURING MANAGER Mark Cirillo
ILLUSTRATION COORDINATOR Gene Aiello

This book was set in 10/12 Palatino by Publication Services and printed and bound by Courier Westford. The cover was printed by Courier Westford.

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Library of Congress Cataloging in Publication Data:

Alexopoulos, Constantine John, 1907–1986
Introductory mycology / C. J. Alexopoulos, C. W. Mims, M. Blackwell. – 4th ed.
p. cm.
Includes bibliographical references.
ISBN 0-471-52229-5 (cloth : alk. paper)
1. Mycology. I. Mims, Charles W. II. Blackwell, Meredith. III. Title.
QK603.A55 1996
589.2–dc20 95-20699
CIP

Printed in the United States of America.

10 9 8 7 6 5 4 3 2

PREFACE

Since the Third Edition of *Introductory Mycology* was published in 1979 the organisms commonly known as fungi have been recognized for their utility in developing and testing many kinds of hypotheses, as model systems in biology, and as creatures of pure beauty and delight despite misconceptions in a somtimes mycophobic world. Applications of modern research techniques, biomedical, agricultural and industrial concerns, and increased awareness of various ecological and phylogenetic issues all have helped to contribute to an explosion of knowledge relating to fungi and all have a base in traditional mycology. Both the amount and diversity of this knowledge presented a dilemma and made it inevitable that much interesting material would not be covered in this revision. In the end we decided to approach this revision by producing a book from which we ourselves could teach and from which our own students could learn. For us this meant the book would be phylogenetically based in the tradition since the First Edition (1952) written by our major professor C. J. Alexopoulos. We firmly believe that the taxonomic approach provides a framework with predictive value. Therefore the discussions of the many activities of fungi that directly or indirectly impact other living things including humans are discussed in the context of their close relatives. We hope that you will use the index to search out ecological topics such as "endophytes," "plant pathogens," "medically important fungi," and "dispersal" or genetics information such as "mating types" and "vegetative compatibility" that may appear in several chapters.

In a vigorous field there is never a good time either to write or to revise a textbook. The timing was particularly bad for us because of the rapid developments occurring in the area of fungal systematics. While it might have been wise for us to wait a few years for the air to clear we decided to proceed with the project and do the best job we could based on the data currently available. However because we did not want to clutter the literature with many new names we chose to use a less than formal taxonomic scheme especially at higher taxonomic levels. Instead the phylogenetic trees are indicative of these related groups as they are understood currently.

Based on the best phylogenetic information available the kingdom *Fungi* includes four phyla: *Chytridiomycota, Zygomycota, Ascomycota,* and *Basidiomycota.* Other organisms traditionally known as fungi (*Oomycota, Hyphochytriomycota*) and four groups sometimes called slime molds are not closely related to kingdom *Fungi* but we often will refer to all of these groups as fungi. Because these organisms all occur in the usual habitats of *Fungi* and have similar modes of nutrition a mycologist or plant pathologist would be incomplete without knowledge of them. We therefore have provided a rather complete coverage of all the organisms traditionally considered as fungi so that a mycologist now can be described as someone who studies fungi not only *Fungi.* As you might have noticed formal taxa at all levels are italicized. This will avoid confusion over what is a formal name, a device suggested by the most recent *International Code of Botanical Nomenclature.* You also may have noticed that we mentioned "phylum," and the Code now allows this substitution for the category "division."

Is the book too heavy? This is equivalent to saying it contains too much knowledge about fungi. Our experience in teaching mycology tells us that it is difficult to cram as much as we would like into a term. But we also know that many students want to learn a great deal more about fungi than we can cover in a single course whatever the length of the term. For this group of students we say, read on! However with practical considerations in mind we did our best to produce a book that could be used effectively in different ways. For example the first three chapters as well as those chapters and chapter sections that introduce the various phyla should be appropriate for shorter undergraduate and graduate courses alike. Other sections of the book relating to specific groups of fungi are considerably more detailed but should permit interested students to delve more deeply into some groups of fungi. The intent of so many cited references is to lead students into mycological literature. The numerous illustrations, life cycle drawings, and tables should be useful to students at all levels. A number of the drawings included in this edition were retained from the previous edition of the book while new drawings were skillfully prepared by Carol Gubbins Hahn. Although we prepared many new photographs specifically for this text, others were graciously supplied by workers from many parts of the world who are acknowledged in the figure legends. Many individuals also devoted much time and effort to reviewing chapters for us and answering many questions. Because of this input the book is truly a joint effort of the mycological community at large. Any mistakes or shortcomings you find are, however, ours alone.

During the three years of preparation of the Fourth Edition we increasingly relied on computerized data bases and on the Internet. It is possible to communicate almost instantly with any mycologist anywhere in the world as long as that mycologist has an electronic mail address. We recommend that every student become familiar with the mycological resources such as those listed on the Mycological Home Page of the World Wide Web. There you will find such listings as type specimens of fungi in certain herbaria, addresses, newsletters including that of the Mycological Society of America, and directions to get to other listings of mycological interest. Another valuable resource provides DNA sequences of organisms that have been submitted to the data bases that collect this type of information along with the reference and, often, an abstract if it has been published. Information on cultures in almost any culture collection in the world is readily available. Meeting abstracts also now are circulated this way. Much of this information is available much sooner than or even in place of publication of hard copies. In fact we would appreciate hearing about any suggestions you might have for the revision of this edition by e-mail.

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April 10, 1995

ACKNOWLEDGEMENTS

We truly are indebted to a large number of individuals who assisted us in the preparation of the Fourth Edition of *Introductory Mycology*. This includes all the people who so willingly contributed illustrations as well as the various journals, book publishers, and professional organizations that granted us permission to use copyrighted materials. We also are especially grateful to the individual scientists who took time to review chapters for us. These include S. L. Anagnostakis, M. E. Barr, G. L. Benny, M. L. Berbee, R. A. Blanchette, J. P. Braselton, R. S. Currah, J. W. Deacon, M. S. Fuller, B. J. Goates, D. L. Hawksworth, T. J. A. Hedderson, D. S. Hibbett, R. A. Humber, K. G. Jones, S. Kroken, C. P. Kurtzman, R. W. Lichtwardt, L. J. Littlefield, G. M. Mueller, H. Nishida, E. Parmasto, D. H. Pfister, D. Porter, M. Powell, D. R. Reynolds, J. D. Rogers, G. S. Saenz, E. R. Siegel, L. Sigler, E. G. Simmons, K. M. Snetselaar, J. W. Spatafora, C. Staben, J. Sugiyama, J. W. Taylor, S. C. Tucker, and K. Wells. R. L. Gilbertson read a number of chapters. In particular, we acknowledge G. L. Benny for his assistance in writing parts of Chapter 5 on *Zygomycetes* and K. G. Jones for assistance in writing parts of several discussions on fungal genetics. Those individuals who provided literature (often unpublished) and answered numerous questions include J. F. Ammirati, J. B. Anderson, J. C. Bailey, D. J. S. Barr, G. L. Barron, R. A. Blanchette, T. D. Bruns, G. C. Carroll, S. C. Cassar, R. L. Chapman, P. R. Crane, K. J. Curry, H. C. Evans, R. Fogel, M. Galun, A. Gargas, D. M. Geiser, A. Hajek, T. C. Harrington, G. Hausner, G. S. de Hoog, J. W. Kimbrough, L. M. Kohn, R. P. Korf, K. J. Kwon-Chung, D. J. McLaughlin, D. Malloch, D. L. Nuss, F. Oberwinkler, M. E. Orlowski, M. E. Palm, R. H. Petersen, A. D. M. Rayner, S. A. Redhead, S. A. Rehner, R. D. Rosing, A. Y. Rossman, G. J. Samuels, K. A. Seifert, R. C. Summerbell, B. C. Sutton, E. C. Swann, T. N. Taylor, A. Tehler, D. TeStrake, S. Turner, R. C. Ullrich, J. F. White, and M. J. Wingfield.

The assistance and patience provided by Cathy Donovan, Editorial Program Assistant, John Wiley and Sons, Inc., our closest contact during the duration of this undertaking, were remarkable and we thank her for her enormous effort. Beatrice Ruberto did the copyediting of the manuscript and although we came to loathe her nagging queries in the margins we are now very happy she caught so many of our errors. Sandra Russell, Senior Production Editor, was responsible for getting the copy edited version past that messy stage and helped us to eliminate many errors and generally tie up loose ends. In addition Sally Cheney and David Harris, our editors at Wiley, helped in ways we never knew. Laura Nichols is responsible for the design and layout of the book. Gene Aiello was the illustration coordinator. The massive amounts of typing were skillfully accomplished by Rosemary Wood from the University of Georgia, and Karen LeBlanc and Priscilla Milligan from Louisiana State University; their hard work, attention to detail and unfailing good humor greatly facilitated our efforts. MB also typed with less good humor. Sarah Larsen helped a lot with the final proofing. It was a pleasure to work with Carol Gubbins Hahn whose experience in drawing fungi made explaining what we wanted easy.

Finally CWM thanks his wife Sandy for her support, patience, and love during the three years that it took to finish this task. This was her second tour of duty with "the book," a fact that probably qualifies her for a medal of some sort—perhaps even a purple heart! MB thanks her mother Renée May who fed her and, along with Élise and David Bajo, encouraged her throughout the project. She also thanks Kevin G. Jones who was valiant in his efforts to keep the lab functional and tidy. We thank Juliet Alexopoulos for her friendship.

This book is dedicated to our fathers John J. Mims (1914–1989) and Robert E. May (1911–1994) who gave us early lessons on the natural history of southwestern Louisiana and to our mycological forebearers and descendants

A. de Bary (1831–1888)

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W. G. Farlow (1844–1919)

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B. M. Davis (1871–1957)

|

F. L. Stevens (1871–1934)

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C. J. Alexopoulos (1907–1986)

C. W. Mims	*M. Blackwell*
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E. C. Swann	
J. Kerrigan	
J. Taylor	
K. M. Snetselaar	

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Kingdom *Fungi*

Introduction to Fungi and Their Significance to Humans

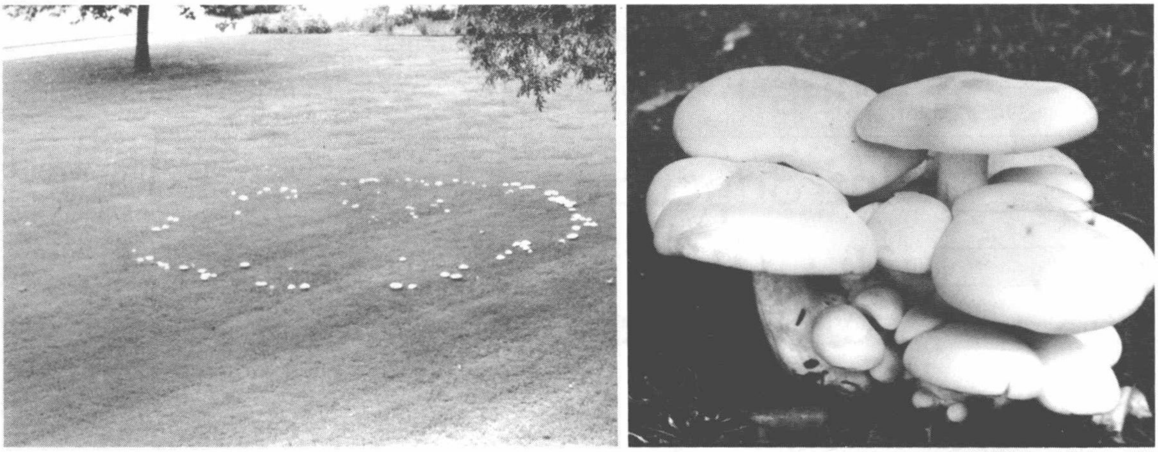
Three and one-half millennia ago, so the legend goes, the Greek hero Perseus, in fulfillment of an oracle, accidently killed his grandfather, Acrisius, whom he was to succeed on the throne of Argos. Then, according to Pausanias,[1] "When Perseus returned to Argos, ashamed of the notoriety of the homicide, he persuaded Megapenthes, son of Proetus, to change kingdoms with him. So when he received the kingdom of Proetus he founded Mycenae, because there the cap (*mykes*) of his scabbard had fallen off, and he regarded this as a sign to found a city. I have also heard that being thirsty he chanced to take up a mushroom (*mykes*) and that water flowing from it he drank, and being pleased gave the place the name of *Mycenae*."[2]

Thus, one of the greatest civilizations ever developed, the Mycenaean, may have been named for a legendary mushroom (Fig. 1-1). Derived from the same Greek word, *mycology* (Gr. *mykes* = mushroom + *logos* = discourse), etymologically, is the study of mushrooms.[3] And, indeed, that is how mycology began in the dim past, for the mushrooms are among the largest fungi and attracted the attention of naturalists before microscopes or even simple lenses had been thought of. With the invention of the microscope by van Leeuwenhoek in the seventeenth century the systematic study of fungi began, and the man who deserves the honor of being called the founder

[1]See Frazer's translation (1898) of Pausanias (Ramsbottom, 1953).

[2]Quoted by permission of Macmillan and Co., London.

[3]Actually, the word **mycology** is an improperly coined term. The correct word is **mycetology,** inasmuch as the combining form of *mykes* is **myceto,** in accordance with the principles of Greek grammar.



(A) (B)

Figure 1-1 Mushrooms, the spore-producing structures of certain fungi: (A) typical "fairyring" of mushrooms produced on a lawn; (B) higher magnification view of a cluster of mushrooms. (Photographs by C. W. Mims.)

of the science of mycology is Pier' Antonio Micheli, the Italian botanist who, in 1729, published *Nova Plantarum Genera,* in which his researches on fungi were included.

But what are fungi? To define the exact limits of the group is very difficult. Traditionally, biologists have defined fungi as eukaryotic, spore-producing, achlorophyllous organisms with absorptive nutrition that generally reproduce both sexually and asexually and whose usually filamentous, branched somatic structures, known as hyphae, typically are surrounded by cell walls. This is perhaps as good a definition as any, but like all definitions, it is not watertight. In addition, it has become increasingly apparent in recent years that the organisms traditionally referred to as fungi are not all closely related. This has prompted some authors (Bruns et al., 1991) to use the term "fungi" in a very general sense and the term "Fungi" with a capital *F* specifically for the so-called true fungi that appear to be related to one another. In this textbook, we will take a very broad approach and will discuss all the major groups of organisms that have been called fungi over the years as well as some other organisms, such as the slime molds, that historically have been studied by mycologists. To help in the identification of formal groups, we use the increasingly popular convention of italicizing all scientific names regardless of rank.

In this book we place the true fungi in the kingdom *Fungi,* which includes the phyla *Chytridiomycota, Zygomycota, Ascomycota,* and *Basidiomycota.* Additional phyla that will be considered include *Myxomycota, Dictyosteliomycota, Acrasiomycota,* and *Plasmodiophoromycota* of the polyphyletic protista and the *Stramenopila* phyla *Oomycota, Labyrinthulomycota,* and *Hyphochytriomycota* (see Chapter 3). The remainder of this chapter serves primarily as an introduction to members of the kingdom *Fungi.* Included in this kingdom are forms commonly known as mushrooms, boletes, bracket or shelf fungi, powdery mildew fungi, bread molds, yeasts, puffballs, morels, truffles, and the smut and rust fungi, just to name a few.

The fungi constitute a very large group of organisms found in virtually every ecological niche. Hawksworth (1991) estimated that on a worldwide basis there are about 1.5 million species of fungi. To date, however, only about 69,000 species have been described. The tremendous discrepancy between the numbers of known versus estimated species appears to relate to the fact that there has been woefully inadequate sampling of fungi in many parts of the world, most notably tropical and subtropical regions. Currently there is tremendous interest in and actually a sense of urgency about documenting the world's fungi. This is coming about at the same time that we are beginning to see reports concerning alarming decreases in both the total number of fungal species and the quantity of individual species in Europe (see Cherfas, 1991). In the case of tropical and subtropical regions it would indeed be a tragedy to lose species to extinction before we even have determined that they exist. This is, however, more than just a philosophical or ethical concern. Fungi are extremely valuable sources of chemicals, including various antibiotics, and also have great potential as biological controls for many serious pests. As noted by Hawksworth (1991), "the world's undescribed fungi can be viewed as a massive potential resource which awaits realization."[p. 650]

Importance of Fungi. The systematic study of fungi is only 250 years old, but the manifestations of this group of organisms have been known for thousands of years—ever since the first toast was proposed over a shell full of wine and the first loaf of leavened bread was baked. Indeed, ancient peoples were well aware of biological fermentation. Although we now know that fermentation is accomplished by certain single-celled fungi known as yeasts, the Egyptians considered fermentation the gift of the great God Osiris to mankind. The ancient Greeks and Romans worshipped Dionysius and Bacchus and celebrated the Dionysia and the Bacchanalia, great festivals in which wine flowed freely. The Romans attributed the appearance of mushrooms and truffles to lightning hurled by Jupiter to the earth. Even in modern times, the native peoples of Mexico and Guatemala believe that the appearance of certain mushrooms such as the fly agaric (*Amanita muscaria*) is somehow correlated with thunder and lightning. The role that mushrooms play in the religion and mythology of endemic Mexican and Guatemalan peoples (Fig. 1-2) is well documented by Lowy (1971, 1974, 1977), and the use of the hallucinogenic mushroom *Psilocybe cubensis* in the religious rites in some parts of Mexico has been interestingly described by various authors including Wasson (1980) and Wasson et al. (1974). Many other examples of the association of fungi with the supernatural by primitive peoples throughout the world can be found in Wasson and Wasson (1957). A case reported from North America involves the use of spirit figures carved from the large, hard sporophores of the wood-rotting species *Fomitopsis officinalis* by some indigenous peoples of the northwest coast of the United States (Blanchette et al.,

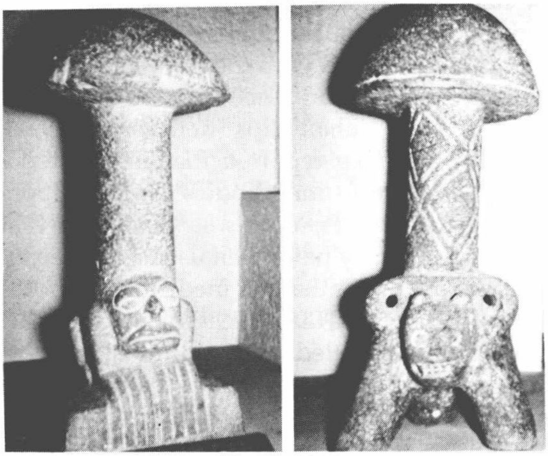


Figure 1-2 Two mushroom stones, possibly used in religious ceremonies or simply as art objects from the Middle Preclassic (± 1000–300 B.C.) of Mesoamerica. Human effigy (left): height 32 cm, cap diameter 15 cm. Both at the Museo de Antropologia, Guatemala. (Courtesy B. Lowy.)

Figure 1-3 Bioluminescent fruiting bodies of the mushroom ***Mycena lux-coeli*** photographed by their own light. (Photograph by Y. Haneda. By permission of Worth Publishers.)

1992). These figures apparently were placed on Shaman graves as guardians. Sporophores of this same fungus were used as medicines by native peoples of North America (Blanchette et al., 1992). In this regard it also is interesting to note that what were originally described as "chunks of antibiotic fungus strung on leather tongs" were found with the frozen remains of the Stone Age man discovered in a melting glacier in the Italian Alps (Rensberger, 1992). It since has been reported that this material consists of the fruiting bodies[4] of a polypore by the name of *Piptoporus betulinus* and that this material may have been used as tinder for fire making rather than for medicinal purposes (see Chapela and Lizon, 1993); however, this matter is not settled. For additional insights into some of the more curious features of the relationships of fungi with humans and other organisms see Findlay's (1982) small book titled *Fungi: Folklore, Fiction & Fact* and Brodie's (1978) *Fungi—Delight of Curiosity*.

In regard to fungal folklore and the general mystique of fungi, we should mention the topic of bioluminescence in these organisms. The reproductive structures produced by some species (Fig. 1-3) and, in some cases, wood permeated by hyphae actually may give off visible light causing them to glow in the dark. This phosphorescent glow has long fascinated and even frightened humans, and much has been written about the subject (see Glawe and Solberg, 1989). Observations on bioluminescent fungi can be traced as far back as Aristotle (Harvey, 1957). Apparently, people have long used pieces of bioluminescent wood to mark their paths at night, and there even are reports of soldiers attaching pieces of luminous rotten wood to their helmets in order to be visible to one another at night (see Glawe and Solberg, 1989). In the United States the glow produced by bioluminescent fungi has been referred to as "foxfire." For information on some of the North American species of bioluminescent fungi see O'Kane et al. (1990). One of the

[4]Spore-producing structures of fungi often are referred to as **fruiting bodies.**

better known species is the so-called Jack-O-Lantern mushroom, whose orange gills glow in the dark.

Unfortunately for the discipline of mycology, few individuals realize how intimately our lives are linked with those of fungi. However, it truly can be said that scarcely a day passes during which all of us are not benefitted or harmed directly or indirectly by these inhabitants of the microcosm. For example, if you are much under the age of 50, it is probably difficult for you to comprehend how many lives have been saved by penicillin. This antibiotic was not widely available until its development was hastened by World War II. At least one prominent mycologist we know of probably was saved from meningitis just as the antibiotic became available. Before penicillin was available, an infection even from a scratch might sometimes lead to amputation of a limb or even death. It is possible that you too may have survived to study fungi because of a fungal antibiotic. It is obvious that individuals who study fungi must do a better job of educating the general public about the importance of these organisms. Perhaps the first step is simply to try and improve overall public awareness of fungi. One example of a recent event that probably has done more along these lines than anything else in many years was the report by Smith et al. (1992) that *Armillaria bulbosa*,[5] a fungal species that is a facultative parasite of tree roots, may be among the largest and oldest living organisms. This report not only was highlighted in the scientific press (Brazier, 1992; Gould, 1992), but also was reported widely in newspapers in North America and Great Britain. Basically, what Smith et al. (1992) reported was that one clone of *Armillaria bulbosa*—dubbed "fungus humongous" by the popular press—occupies a minimum of 30 acres in a Michigan forest and that the thallus or body of the organism weighs in excess of 10 tons.[6] The age of this thallus was estimated to be more than 1500 years. This report has, of course, stimulated much discussion about what the exact definition of an individual should be (Gould, 1992), and while it may or may not be fair to compare this clone of *Armillaria bulbosa* to whales, giant redwoods, and bristle cone pines, it nonetheless has been exciting to see a fungus discussed in reference to such notable creatures.

Figure 1-4 provides an overview or summary of many of the activities of fungi that affect us for either better or worse. Most of the topics highlighted in this figure will be considered individually at various places in this book. In this introductory chapter about all we can do is simply introduce you to a few of these topics. As you examine this figure, it is important for you to keep in mind that the single most important role that fungi play in our ecosphere is not specifically identified. Without doubt, however, fungi are most important on Earth as agents of decay. This is particularly true in forest ecosystems where fungi are the principal agents that decompose cellulose and lignin, the primary components of wood (Figs. 1-5A,B). In reality, the biomass production in a forest ecosystem is controlled largely by wood-rotting fungi, as these organisms determine the rates at which nutrients are released back into the ecosystem following the deaths of trees. In his interesting review of the many activities of wood-decaying fungi in North American forests, Gilbertson (1980) discussed the importance of brown rot residues to maintenance of the western U.S. conifer forests. The residues are left after cellulose decomposition by certain fungi.

[5]The correct name of this species appears to be *Armillaria gallica*.

[6]A much larger clone of *Armillaria ostoyae* on ponderosa pine determined by vegetative incomparability criteria previously was reported in the state of Washington (Shaw and Roth, 1976) but did not receive the attention that the Michigan clone of *Armillaria* has.

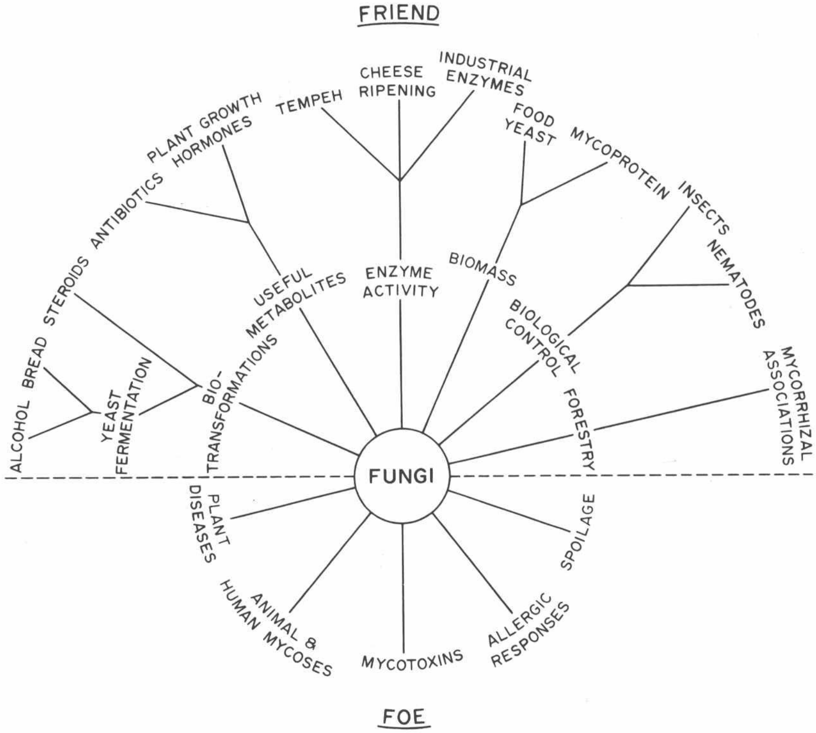
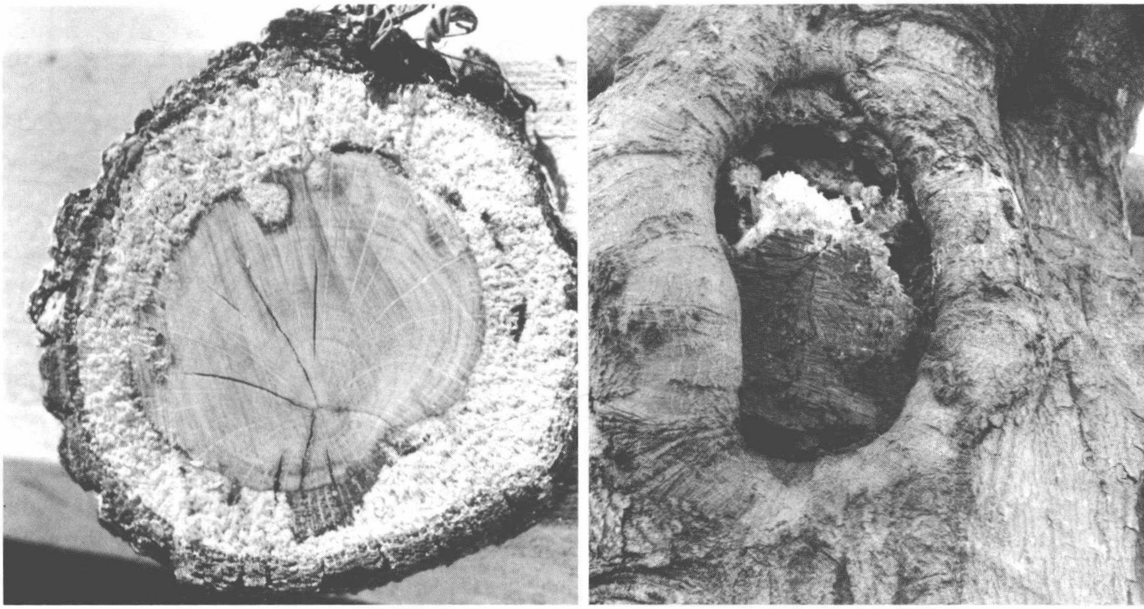


Figure 1-4 Summary of the activities of fungi as they relate to humans. [From Moss (1987) by permission of the British Mycological Society.]

In addition to their importance as decomposers in forest ecosystems, fungi also are directly responsible for the destruction of a wide variety of wood products, including lumber, railroad ties, and telephone poles. Unless wood products are protected from moisture or treated with preservatives, they are almost certain to be attacked by various wood-rotting fungi. The costs associated with our efforts to protect wood products from decay is staggering A particularly notorious wood-rotting species is *Serpula lacrimans,* which causes a condition commonly known as dry rot. During the days of wooden warships, this fungus was a major cause of serious and widespread decay of sailing vessels (see Findley, 1982). In this regard, one James Sowerby (1757–1822) is said to have been the first consulting mycologist, having been hired by the Royal Navy to reduce losses to decay in British warships. Even today, *S. lacrimans* is still important, primarily in Europe, where the dreaded dry rot causes tremendous damage to wooden structural elements and floors in houses and other buildings. The destructive effects are comparable to termite damage done to wooden structures in the United States.

Because fungi can utilize so many different substrates as food (Fig. 1-6), they are capable of attacking many products we utilize, including fabrics, leather goods, various petroleum products (including certain fuels and lubricants), and of course, almost all foodstuffs. In our efforts to protect our foods from fungi—and



(A) (B)

Figure 1-5 (A) Section of a large branch of an oak tree showing the rotting caused by a fungus. (B) Rotted remains of the base of a pruned oak limb. The fungi responsible for this type of decay create cavities in trees that provide homes for various animals. (Photographs by C. W. Mims.)

of course, bacteria—we have employed a variety of approaches, including salting, drying, freezing, heating, canning, irradiation, and the use of chemical additives. Besides simply spoiling foods, certain species of fungi also produce some very toxic substances known as **mycotoxins** on certain plant materials that we either consume directly as food or feed to our animals.[7] Particularly noteworthy examples are the ochratoxins produced on cereal grains by *Aspergillus ochraceus* and *Penicillium viridicatum,* the aflatoxins produced by *A. flavus* and *A. parasiticus* on various nuts and grains (notably peanuts, pecans, corn, and millet), and the fumonisins produced on corn by *Fusarium moniliforme.* The ochratoxins have been implicated in a type of human renal atrophy endemic to households in Bulgaria, Romania, and the former Yugoslavia (Mantle and McHugh, 1993), while aflatoxins have been found to cause cancer in all species of animals tested and are among the most potent carcinogenic compounds yet identified (see Ames et al., 1987). The consensus at this time seems to indicate that aflatoxins also cause liver cancer in humans, and presently these compounds are the only mycotoxins regulated in food in the United States. Interestingly, aflatoxins show up not only in plant materials but also in animal-based foods we consume such as meat, eggs, and dairy products. The fumonisins only recently have begun to receive attention but thus far have been implicated in human esophageal cancer, a fatal neurological disease of horses, and a

[7]For an introduction to the topic of mycotoxins see "Mycotoxins: Economic and Health Risks," Council for Agricultural Science and Technology, Report No. 116, November 1989.