

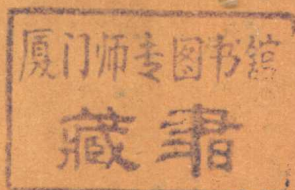
Introductory Mycology

THIRD EDITION

▪ 11089

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Charles W. Mims



Introductory Mycology

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Preface

An informal survey of a number of teachers of mycology in the United States, some young, and some more experienced, revealed that the morphology/taxonomy approach is still widely used in introductory mycology courses for graduate and undergraduate biology, botany, microbiology, and plant pathology majors for which this book has been used in the two previous editions. This approach coincides with our own views and will continue to be the basis of this book. Although we found it desirable to introduce some physiological, biochemical, genetic, and ecological data in a few places, we have kept these to a minimum so as not to expand the book unduly and to allow the text to remain introductory. We still feel that a student needs to know how fungi are constructed and how they reproduce before studying their biochemistry and ecology.

In a morphological/taxonomic discussion of the fungi, the system of classification used becomes, of course, of paramount importance. Since the second edition of this book was published, a number of systems have been proposed, but none has been universally accepted. The one view many mycologists seem to hold is the removal of the fungi from the Kingdom Plantae into a kingdom of their own. We call this kingdom **Myceteae** and subdivide it into the more or less traditional Divisions, Subdivisions, Classes, and Subclasses that we discuss in the usual sequence. Our only major deviation from tradition—if it be regarded as such—is the separation of the Oomycetes from

other flagellate fungi into the Subdivision Diplomastigomycotina.

We have completely rewritten and updated most chapters in accordance with modern taxonomic proposals. In treating the Myxomycetes in considerable detail, we have been influenced by their neglect in all other textbooks of mycology in English and we cannot conceive of an introductory mycology course that omits them. Besides, our own interest in these organisms is well known! We have considered discussing the lichenized fungi together with the nonlichenized, which they resemble, but finally decided to treat them separately, as in the last edition, but in a little more detail.

We have kept phylogeny out of this book. To claim we know how fungi are related would be foolish. As long as mycology remains alive, new data about the fungi will continually become available and our present phylogenetic ideas will become obsolete. Why burden the student with our own conjectures about fungal relationships? Individual instructors can teach their own views without interference from us.

On the matter of illustrations we have retained most of the life cycle drawings, updating them when necessary, because students found them so useful in previous editions. We have added some new drawings, ably executed for this book by Dr. Raymond W. Scheetz, and a number of photographs and electron micrographs, both scanning and transmission, to illustrate important structures.

We express gratitude to all colleagues who have

critically read portions of the manuscript and we have incorporated many of their suggestions. We alone, however, are solely and jointly responsible for any errors of fact or judgment that appear in

Austin and Nacogdoches, Texas
March 1, 1979

this book. We shall always welcome suggestions from both teachers and students for the improvement of possible subsequent editions.

CONSTANTINE J. ALEXOPOULOS
CHARLES W. MIMS

Acknowledgments

We want to thank all authors, editors, and publishers of books and journals who permitted us to quote passages and use illustrations from published works as credited. We also wish to extend our thanks to those who provided glossy prints of illustrations, some of which are published here for the first time. We are especially pleased to acknowledge the help of Dr. Raymond W. Scheetz, Department of Biology, University of Southern Mississippi, for the many fine drawings, photomicrographs, and scanning electron micrographs he produced especially for this edition, to supplement the artwork of Dr. Sung-Huang Sun.

Thanks are also due to a large number of mycologists who helped with the literature and who made important suggestions for the treatment of certain fungal groups. In this connection, we want particularly to acknowledge, among others too numerous to mention, the help of Drs. Henry Aldrich, S. Bartnicki-Garcia, L. S. Batra, R. K. Benjamin, Meredith Blackwell, H. J. Brodie, G. C. Carroll, G. T. Cole, Y. Hiratsuka, J. W. Kimbrough, C. L. Kramer, E. S. Luttrell, D. Malloch, K. B. Raper, D. R. Reynolds, J. D. Rogers, R. Seymour, Martha Sherwood, W. G. Soren-

son, P. Szaniszló and Mr. R. Slocum. We are greatly indebted to Mrs. Betty White, Librarian of the Science Library, University of Texas at Austin, without whose help in locating literature, this book could not have been completed for publication as scheduled.

We are especially grateful to the following mycologists who read critically portions of the manuscript before the final draft was prepared: Drs. L. R. Batra, R. K. Benjamin, G. L. Benny, G. C. Carroll, O. R. Collins, M. S. Fuller, T. M. Hammill, R. A. Humber, R. W. Lichtwardt, S. T. Moss, K. B. Raper, D. R. Reynolds, J. D. Rogers, Roland Seymour, Paul L. Szaniszló, J. S. Trappe, and Mr. R. Slocum.

Finally, we thank our wives Juliet Alexopoulos and Sandy Mims for offering many suggestions for the clarification of the writing and for their patience and understanding during the years required to complete this new edition.

This book was edited by Rosemary Wellner. To her we express our gratitude for her very careful editing, and for putting up with our idiosyncrasies with unusual understanding.

Preface

To The Second Edition

Progress in mycology has been so pronounced in the last ten years, and the first edition of this book has been so kindly received by students and teachers throughout the world, that I have felt compelled to revise the text in accordance with newer findings.

The new edition is no different from the first in its general approach to the study of fungi. Morphology and taxonomy continue to form the basis of discussion. However, significant physiological and genetic knowledge is interwoven with the morphological and taxonomic wherever it can be discussed on an introductory level.

Rising costs of production have made it necessary to eliminate some of the features that seemed desirable in the first edition. Thus, the chapter on bacteria was regrettably omitted, and the summaries at the ends of the chapters were eliminated. For the same reason, the number of references has been kept relatively small.

Two features of the first edition which students particularly praised: the inclusion of derivations of mycological terms in the text, and the illustrated life cycles, are retained.

Although this book was originally written to serve an undergraduate course, it has been widely adopted as a text in graduate courses as well. This fact influenced my decision to deal with some subject matter at a higher level than in the first edition; to introduce new groups, such as the Labyrinthulales, the Hyphochytridiomycetes, and the Tricho-

mycetes; and to document the text much more thoroughly.

In an essentially morphological-taxonomic book, the system of classification adopted is, of course, of considerable importance. The phylum Myxomycophyta is no longer recognized. The Acrasiales and Labyrinthulales are treated as orders of uncertain affinity and are not included in any class or division. The Myxomycetes and the Plasmodiophorales are treated as classes of the Division Mycota.

For many years mycologists have recognized that the Phycomycetes are a heterogeneous group of fungi. In 1958 Sparrow pointed out that the aquatic Phycomycetes consisted of several distinct "galaxies" to which he gave names with class endings. These galaxies are here recognized as classes, and the concept is expanded to include the non-aquatic groups. Sparrow used the term Phycomycetes for one of these galaxies. I am substituting Oömycetes as a class name for this group. Phycomycetes has been so well established in its wider sense that to give it a new restricted meaning would be inadvisable. Furthermore, those who agree with the principle of this classification, but who prefer not to discard the Phycomycetes as a group, may treat the classes in this book as sub-classes under the class Phycomycetes.

In treating the Ascomycetes I have essentially followed Martin's new key in Ainsworth's *Dictionary of the Fungi*, deviating from it in certain

places. I have adopted Luttrell's sub-classes: Hemiascomycetidae, Euascomycetidae, and Loculoascomycetidae, using name endings recommended by the code, and have retained his convenient subdivision of the Euascomycetidae into four series: Plectomycetes, Pyrenomycetes, Discomycetes, and Laboulbeniomyces. I have deviated from both Luttrell and Martin in retaining the name Sphaeriales for the order they call Xylariales and in recognizing the Clavicipitales.

The chapter on the Deuteromycetes has been considerably expanded to include a discussion of the parasexual cycle, to inform the student of the new and rapidly spreading ideas on the classification of the Hyphomycetes, and to give somewhat more attention to the medical fungi than was given in the first edition.

In my treatment of the Basidiomycetes I have followed Martin but have included the Sporobolomycetaceae in this class instead of in the Deuteromycetes.

Some of my colleagues will again regret the absence of phylogenetic diagrams and the very limited phylogenetic discussions. The more I study the fungi the more uncertain I become about their relationships. I prefer, therefore, not to share my burden with students who are just beginning the study of fungi.

Austin, Texas
July, 1962

I was fortunate in securing once again the talented services of Dr. Sung-Huang Sun, who prepared the drawings for both editions. I wish to express my appreciation to her and to those colleagues who furnished me with glossy prints of photographs or electron micrographs of fungi.

I owe special thanks to Professors Jules Brunel of the University of Montreal and Donald P. Rogers of the University of Illinois, who, after reading the first edition from cover to cover, furnished me with long lists of comments, corrections, and suggestions, and to Professor Ralph Emerson of the University of California for his list of suggestions regarding the treatment of the lower fungi. I am particularly grateful to Professor G. W. Martin of the University of Iowa for his suggestions on the section dealing with the Heterobasidiomycetidae and for his willingness to take time on numerous occasions to discuss with me special problems on the classification of the fungi. From both teachers and students I shall continue to welcome suggestions which may help improve subsequent editions.

Once again my wife has been of the greatest help in judging the clarity of presentation. For her help, her encouragement, and her patience I am grateful.

CONSTANTINE J. ALEXOPOULOS

Preface

To The First Edition

Ever since my student days, more than two decades ago, I have recognized the need for a textbook in Mycology written for the student who knows nothing about the fungi and who needs an orderly presentation of certain fundamental facts on the structure and classification of these organisms in the form of broad concepts and patterns, without the innumerable details and exceptions which make the study of fungi so fascinating for the specialist, but so bewildering for the beginner.

With the discovery of antibiotics, with the recent strides in the genetics and the biochemistry of the fungi, and with the realization of the role which fungi play in the causation of allergies and parasitic diseases of man, the need for a textbook written on the elementary level has become greater rather than less, for some knowledge of mycology is now not only necessary to the biologist in general, but is becoming a part of the cultural background of every educated and well-informed individual. It should be possible then to give the student an insight into the importance of fungi to man and into the structure, life history, and classification of the fungi in general without "telling all."

Although few people dispute, I believe, the need for an elementary text in this field, there is certainly no agreement as to the general approach which such a text should take. This, of course, is the age of biochemistry. The physiological and ecological approach is in vogue all the way from

the kindergarten to the university, and function has replaced structure as the *raison d'être* of biological teaching. This, of course, is as it should be except for the undisputed fact that a beginning student understands function only through the structural features associated with function. He does not see photosynthesis; he sees leaves, oxygen bubbles, and, eventually, chloroplasts; he does not see parasitism; he sees hyphae among host cells, haustoria which have invaded the cells, and symptoms in the form of leaf spots, twig cankers, or skin lesions, and sores; he does not see percentages of oxygen, nitrogen, phosphorus, and carbon, but rather the fascinating streaming of the plasmodium of *Physarum polycephalum* and *Fuligo septica*; he does not see genes A and a, but rather the two colonies which grow together and form the zygospores of *Phycomyces* or the ascocarps of *Neurospora*. In order for function to have any concrete meaning—and remember, we are speaking of the beginning student—a knowledge of general structure and probable relationships, and a working knowledge of terminology, the language of the science, it seems to me, are essential. In this book, therefore, I have discussed the structure of the fungi with stress on the life histories of various representative organisms and have given the basis of what to me appears to be the most acceptable system of classification, with some general remarks concerning the probable relationships of the major fungal groups. The purpose of this book

then is to answer as simply and concisely as possible the question: "What are fungi and how do they affect us?" for the student in agriculture, bacteriology, or other general field of knowledge who has no time and, at this stage of his training at least, no desire to enter into the intricate details of Mycology. I hope that this book also will provide a background, such as can be given in a one-term introductory course for which it is designed, for the student who wishes to make the study of the fungi and their activities his life's work. This book is not a complete treatise on the fungi, and is not intended as a reference book.

So much for the reasons which prompted me to undertake this task. Now a few words in defense of the organization of this book. The chapter on bacteria, which may seem out of place in a book of this type, was included at the express request of a number of my students who think that a brief survey of our knowledge of the structure of bacteria would be at least as useful and as fully justified in a text on Introductory Mycology, as are the chapters on molds and yeasts invariably included in Introductory Bacteriology texts. Certainly I feel that a brief discussion of the Actinomycetes is essential, in view of the great role which these organisms appear to play in the economy of nature and of man, and in view of the fact that they provide a possible link between the bacteria and the fungi upon which it is interesting to speculate.

The chapter on slime molds is included because these organisms are traditionally studied in Mycology and particularly because their intricate structure and great beauty are always sources of interest to the student.

The Deuteromycetes are discussed immediately after the Ascomycetes instead of at the very end of the book as has been customary in other books on Mycology. The dual naming and classification of the Ascomycetes is a difficult concept to teach to beginners and can be taught much better if the classification of the Deuteromycetes is discussed while the imperfect stages of the Ascomycetes are being

studied, and if the Deuteromycetes themselves—those without a perfect stage—are discussed immediately afterward.

The inclusion of the derivations of mycological terms in the text at the time such terms are first introduced and defined rather than in the glossary alone is admittedly experimental. However, the opinion of a number of students consulted is that the advantage of such inclusions as aids in understanding the meaning of the terms far outweighs the possible disadvantage of temporary breaks in thought which parenthetical intrusions may cause.

A feature of the book which I hope will be especially helpful to the beginner is the inclusion of illustrated life cycles for a great many of the species discussed. Although such arrangement of figures requires more space and therefore necessitates a greater reduction in size of the individual drawings than other arrangements, the advantage gained by the presentation of the entire life cycle at a glance more than compensates for the sacrifice in size.

On the subject of classification, I aim to be as conservative as possible when insufficient knowledge of structure and relationships does not warrant acceptance of newer systems of classification, but as modern as possible where newer knowledge has made it advisable to discard older concepts even though such concepts may be well established in the literature. Thus, in the Phycomycetes, I have discarded the Archimycete-Oömycete-Zygomycete concept in favor of the classification based on flagellation, as adopted by Sparrow, Bessey, and Karling. It is my understanding that most Phycomycete specialists in this country have adopted this system. The choice of a classification system for the Ascomycetes was a more difficult task. I have recognized the old and convenient subdivision of the class into two subclasses, the Protoascomycetes and the Euascomycetes, and the subdivision of the latter into Plectomycetes, Pyrenomycetes, and Discomycetes. I have placed the Erysiphales in the Pyrenomycetes because of the arrangement of their asci in the cleistothecium;

many mycologists include them in the Plectomycetes. In treating the Pyrenomycetes, I have followed conservative lines. The main deviations from the traditional system are represented by the inclusion of the Mycosphaerellaceae and the Pleosporaceae in the Pseudosphaeriales rather than in the Sphaeriales, and by the transfer of the Phyllachoraceae—following Miller—to the Sphaeriales. Nannfeldt's classification has been adopted for the Discomycetes except for the inclusion of the family Sclerotiniaceae which most American mycologists now recognize. The traditional subdivision of the Basidiomycetes into Hemibasidiomycetes and Holobasidiomycetes has been followed. The former are discussed under four orders. The Holobasidiomycetes are treated rather briefly. To discuss them more thoroughly would necessitate the introduction of very detailed and difficult material which, I feel, should be left for the more advanced student of Mycology.

Controversial material on classification is introduced at times in order to point out to the student that there are other views on classification besides those which I have adopted, but controversial material is kept at a minimum in order to avoid confusion. I have tried to keep in mind that the student who will use this book will be struggling with a difficult, new terminology and with a mass of new facts, and that, at this stage of his training, he will not be ready to shoulder the burdens of the intended specialist. For this reason, phylogenetic discussion also has been kept at a minimum, but enough is introduced to indicate that we do have some definite, if not always agreed upon, ideas on the origin and evolution of the fungi.

On the matter of references, my policy has been to include: (1) all those cited in the text; (2) all those from which illustrations have been taken; and (3) a few of the most recent articles pertaining to the subject matter in each chapter—even though they may not have been mentioned in the text—to give the interested student a good start toward bibliographical work on any given phase. Very few

references in foreign languages have been included. I should be the last person to deny the value of a knowledge of as many foreign languages as possible in the training of a scientist; but the value of foreign languages and the importance of reading foreign journals do not alter the fact that the American undergraduate who can read a language other than English is indeed unusual. The same is unfortunately true of most graduate students who have not reached the stage of passing the dreaded language examinations which, fortunately, are still required for the Ph.D. degree by most of our graduate schools.

I wish to express my sincere appreciation to all who have aided me in any way. I am especially grateful to my wife, who has given me so many hours, which she would normally devote to her own profession, studying and criticizing the manuscript for clarity of statement and logic of presentation. She has been of the greatest possible help and inspiration throughout the entire task of writing this book. I am thankful to Professor Benjamin Hickok of Michigan State College, who read the entire manuscript and who made numerous editorial suggestions for its clarification. My sincere thanks go to Dr. E. D. Devereux of Michigan State College, who read the chapter on bacteria; to Dr. Leland Shanor of the University of Illinois, who read the chapters on Myxomycophyta and Phycomycetes; and to Dr. Lewis Wehmeyer of the University of Michigan, who read the chapters on Ascomycetes and Deuteromycetes. I alone, however, am responsible for the errors which may be found in this book, and for the views expressed on controversial material. My thanks also go to Mr. Nicholas Mizeres, formerly Assistant in Zoology at Michigan State College, who read the first draft of the manuscript while he was enrolled in my Introductory Mycology course, and who criticized it from the student's viewpoint.

Professors F. C. Strong, E. A. Bessey, and E. S. Beneke of Michigan State College, and Professor J. Arthur Herrick of Kent State University,

have generously contributed a number of excellent color transparencies from which black and white negatives were made. Mr. Philip G. Coleman has taken a number of photographs especially for this book. To all the above I express my gratitude. I am grateful also to all authors of mycological articles who have given me permission to copy illustrations from their respective publications—particularly to those who have furnished me with glossy prints—as well as to the managers, editors, or publishers of the journals or books in which such illustrations have appeared. In order to avoid lengthy and cumbersome legends which would detract from the value of the illustrations in an introductory text, all credit lines for illustrations have been assembled under the section “Acknowledgments” which follows the Glossary at the end of the book. I wish to extend my thanks to The

Michigan State College
January 14, 1952

Science Press, W. B. Saunders Co., Torrey Botanical Club, McGraw-Hill Book Co., Inc., and The Macmillan Co. for permission to use the quotations which appear on pages 50, 50, 75, 124, 320, respectively. Individual credit lines for these quotations appear as footnotes on the pages on which the quotations are used.

Finally I wish to express my appreciation to Mrs. Sung-Huang Sun, formerly Assistant in Botany, Michigan State College, who prepared all the original drawings and who also made all copies from published drawings, and to thank Dr. E. A. Bessey, Distinguished Professor of Botany, Michigan State College, for the many stimulating informal mycological discussions which we have had during the past four years and which have been of great help to me in formulating certain concepts.

CONST. J. ALEXOPOULOS

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Part 1

INTRODUCTION

1

Kingdom Myceteae—Introduction to the Fungi and Outline of the Major Taxa

MOLDS, MILDEWS, YEASTS, MUSHROOMS, AND PUFFBALLS

Three and one-half millennia ago, so the legend goes, the Greek hero Perseus, in fulfillment of an oracle, accidentally 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. 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 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 virtually impossible, for the more we study living organisms the more meaningless our attempts become to delimit any particular group. At present, biologists use the term **fungus** (pl. **fungi**; L. *fungus* = mushroom from Gr. *sphongos* = sponge) to include *eukaryotic, spore-bearing, achlorophyllous organisms that generally reproduce sexually and asexually, and whose usually filamentous, branched somatic structures are typically surrounded by cell walls containing chitin or cellulose, or both of these substances, together with many other complex organic molecules* (Table 1-1, page 11).

form of **mykes** is *myceto* in accordance with the principles of Greek grammar.

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

In simpler words, this means that fungi have typical true nuclei in their cells, that they reproduce by means of spores, and that they have no chlorophyll. It also means that most fungi possess some sort of sexual mechanism, that they have thread-like bodies that usually branch, and that these tubular threads have cell walls that characteristically contain chitin or cellulose or both these substances. This is perhaps as good a definition as any, but, like all definitions, it is not watertight. Some true fungi, for example, are not filamentous, and the filaments of a few others have no cell walls. Some true algae, because they are presumed to have lost their chlorophyll through evolution, fit the above definition rather well but are not fungi. Then there are some organisms mycologists have studied, more or less by default, but which are probably not fungi. They are the cellular and plasmodial slime molds.

In this book, we study mainly the molds and the mildews, the yeasts, the cup fungi, the truffles, the rusts and the smuts, the mushrooms, and the puffballs, and all the other groups we usually include in the fungi. We also devote some time to the slime molds, which in many ways resemble the fungi, and which mycologists usually study.

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. The Egyptians considered it the gift of the great God Osiris to mankind. The ancient Greeks and Romans worshipped Dionysus 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 Indians 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 Mexican and Guatemalan Indian tribes (Figure 1-1) is well documented by Lowy (1971, 1974, 1977) and the religious rights of some of the Indians of Mexico have been interestingly described by Wasson and by Heim and, most recently, by Wasson and coauthors (1974) in various writings about the use of hallucinogenic mushrooms in such ceremonies. Nevertheless, even in today's science-conscious world, a world in which the nucleus of the atom has become a household word, few people realize how intimately our lives are linked with those of the fungi. It can be said truthfully that scarcely a day passes during which all of us are not benefited or harmed directly or indirectly by these inhabitants of the microcosm. Mycologists are indeed poor propagandists.

Fungi play such an important role in the slow but constant changes taking place around us be-

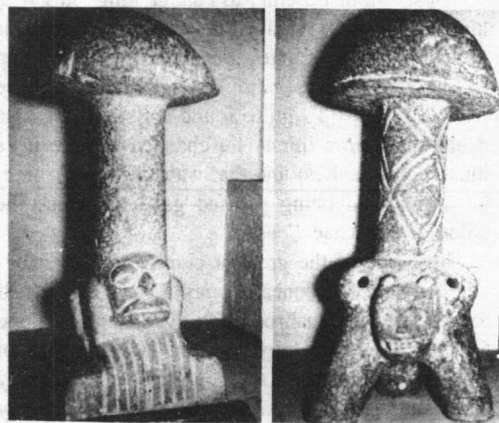


Figure 1-1. Two mushroom stones, possibly used in religious ceremonies or simply as art objects from the Middle Preclassic (± 1000 –300 B.C.). Human effigy (left): height 32 cm, cap diam. 15 cm. Both at the Museo de Antropología, Guatemala. Courtesy B. Lowy.