Mr. Bloomfield's Orchard: The Mysterious World of Mushrooms, Molds, and Mycologists

NICHOLAS P. MONEY

OXFORD UNIVERSITY PRESS

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OXFORD
UNIVERSITY PRESS
2002

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Oxford New York
Auckland Bangkok Buenos Aires Cape Town Chennai
Dar es Salaam Delhi Hong Kong Istanbul Karachi Kolkata Kuala Lumpur
Madrid Melbourne Mexico City Mumbai Nairobi São Paulo
Shanghai Singapore Taipei Tokyo Toronto

and an associated company in Berlin

Published by Oxford University Press, Inc.
198 Madison Avenue, New York, New York 10016

www.oup.com

Library of Congress Cataloging-in-Publication Data
Money, Nicholas P.
Mr. Bloomfield's orchard : a personal view
of fungal biology / Nicholas P. Money.
p. cm. Includes bibliographical references.
ISBN 0-19-515457-6
1. Fungi. I. Title.
QK603 .M59 2002
579.5—dc21 2002072654

1 3 5 7 9 8 6 4 2
Printed in the United States of America
on acid free paper

For Terence Ingold and his jewels

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Preface

> It is indeed a singular and despised family to the history of which we are about to dedicate this volume.
>
> —M. C. Cooke, *British Fungi* (1871)

Some time ago, my colleague Jerry McClure told me that the most fortunate among us are faced with three options at the juncture in life once valued as the midlife crisis: go insane, engage in an extramarital affair, or write a book. In my own approach to this disconcerting landmark, all but the third option vaporized under my wife's guidance. The fruit of her influence is in your hands.

Mr. Bloomfield's Orchard is a personal reflection on the subject of mycology, the scientific study of fungi. Many people giggle at the mention of these organisms, drawing on vague notions about hallucinogens and poisons, fairy tales, and the erectile behavior of mushrooms. Although such peculiarities may draw people to this book, my primary concern as its author is to explore our profound intimacy with fungi and to articulate the most important consequences of these interactions. Employing a flexible interpretation of that term *interaction,* this is a celebration both of the fungi (even the nasty ones) and of a selection of the scientists obsessed with their study (none that I know of have been exceptionally nasty). While I have written for a general audience, particularly those with some scientific education, I also hope to deepen the appreciation of fungi among my biologist peers.

There are a number of people to whom I extend deep gratitude for stimulating this book. As a teenager studying at Bristol University, my first—and most inspiring—guide to mycology was Mike Madelin, and my admiration for my doctoral mentor at Exeter, John Webster, grows with every year. The dedication of this book to Terence Ingold is explained in the narrative. I also thank the staff of the Lloyd Library in Cincinnati for maintaining the world's supreme archive of mycological publications. This book would not have been possible without the sanctuary offered by the Lloyd. Speaking of sanctuaries, Frank Harold was kind enough to offer me one in his laboratory in Colorado at a time when I was lost in New England, and has now shown great generosity in reviewing the *Bloomfield* manuscript. I thank my wife, Diana Davis, for agreeing to marry me, and more pertinently in the context of this book, for her invaluable service as my primary reader.

By discussing fungal processes that I have investigated (if only peripherally), this book has enabled me to revisit my twenty-year journey from student to professional mycologist. I hope you have as much fun reading about this odyssey as I have had recreating it.

Nicholas P. Money
Oxford, Ohio
January 2002

Mr. Bloomfield's Orchard

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CHAPTER 1

Offensive Phalli and Frigid Caps

I am . . . a mushroom
On whom the dew of heaven drops now and then.
—John Ford, *The Broken Heart* (1633)

All sound in the forest is damped by a morning mist trapped under the pine trees on the edge of the moors in Devon, England. Three men are tramping up a steep slope, their boots sinking into the soaking needles. They are searching for eggs. A dead deer smell hangs in the watery air, a hint of sweetness too, and even a suggestion of semen. This odor cannot be ignored. Steamed glasses are wiped every few minutes. The oldest of the men is wearing hunting pants that end at the knees, thick hiking socks bridging the gaps to his red-laced boots. Webster stops, his blue eyes bulging as he scans the forest floor. Squatting, he parts the pine needles and uncovers five pure white eggs, somewhat larger than golf balls. Each is attached to the soil by a branched umbilical cord that snaps as it is tugged away from its siblings. The jelly-filled spheres have cold skins. What monsters will hatch from such spawn? And what is that smell?

A few feet from the nest is a very ugly penis. Poking 6 inches or more from the pine needles, a full erection that arches a little, a pallid shaft protruding from a broken egg. Its head glistens with green-black syrup (Figure 1.1). This is the source of the smell. At the tip, a small hole is circled by a raised ring. Some degenerate must be hiding under the needles and is evidently aroused by the experience. But wait a moment; there are hundreds of these apparitions higher up the slope. Have the collectors wandered into a colony of sexual deviants fixated upon live burial?

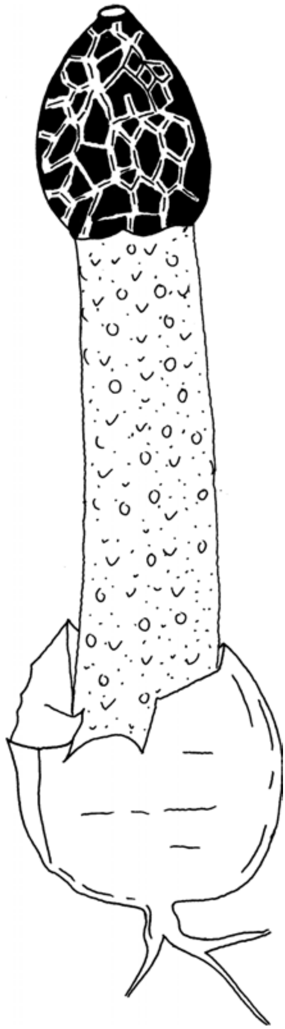

Fig. 1.1 Erect fruiting body of *Phallus impudicus*.

But there are no horny corpses. Little Red Riding Hood's chastity is safe. The erections were accomplished by a fungus whose Latin name is *Phallus impudicus*, the shameless penis, a type of "stinkhorn." You must not forego the spectacle offered by this beast. My first encounter with this bizarre species was made during a foray with the mycologist John Webster (Figure 1.2) and his Spanish assistant Henry Descals. The site on Dartmoor was a favorite of John's, a place he visited every year to collect specimens for his undergraduate classes at the University of Exeter.

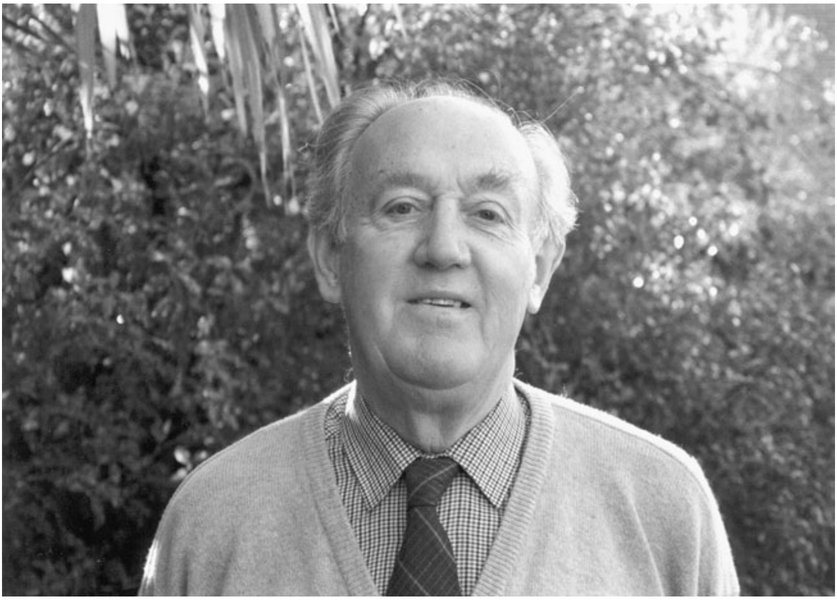

Fig. 1.2 John Webster.

Phallic mushrooms belong to the large group of fungi that includes the more familiar organisms that generate brackets on trees and buttons and portabella caps that end their lives sautéed in olive oil. These organisms are members of a group of fungi called the Basidiomycota,[1] a name that refers to a special kind of spore or microscopic seed called the basidiospore. Thirty thousand species of basidiomycete have been described by scientists, and seventy or so are phallic mushrooms and related fungi that manufacture smelly cages. The phallic ones have proven impossible to ignore. They are featured in Pliny the Elder's thirty-seven-volume *Natural History* written in the first century A.D., a publication with the modest goal of recording "all the contents of the entire world." In his seventeenth-century herbal, John Gerard pictured them in a modest, tip-down orientation, with the following description: "*Fungus virilis penis arecti forma,* which wee English, [call] Pricke Mushrum, taken from his forme." For Victorians in England, sufficiently obsessed with sex to become excited by table legs, their appearance was too much to bear. As a mature woman, Charles Darwin's daughter Etty so despised stinkhorns that she mounted an antifungal jihad with the aid of gloves and a pointed stick. She burned the collections in secret, thereby protecting the purity of thought among her female servants.

The transformation from egg to stinking horn is a slow erection that often begins in the cool of the night and is not complete until sunrise. If an unhatched egg is cut in half, the tissues of the expanded structure are displayed in prefabricated form (Figure 1.3). A hollow shaft of white spongy material called the receptacle runs pole-to-pole through its center. The receptacle is surrounded by the green-black cushion of spores called the gleba, cased in a clear jelly veiled with white skin. When the egg hatches, the receptacle expands by absorbing water and ruptures the skin, carrying the spores on its tip into the air. The jelly lubricates the extending shaft and helps keep the mass of spores in place. The spores are embedded in slime that contains a cocktail of volatile chemicals, including hydrogen sulfide, formaldehyde, methylmercaptan, and unique compounds called phallic acids. Impersonating the smell of rotting flesh, the stinkhorn is irresistible to flies, which swarm on the head, and to slugs, which glide for 20 or more feet for the reward of the cadaverous confection. Within a few hours, the head is cleaned down to the dimpled white surface of receptacle tissue, and the shaft begins to wilt. Although the marathon erection is over, the stinkhorn has been successful. Flies and slugs carry and defecate its spores, whose stinkhorn genes contain the information needed to make more stinkhorns. In common with humans, stinkhorns are here because they are very good at making copies of themselves.

Stinkhorns and other mushrooms are the tips of mycological icebergs. The umbilical cord at the bottom of the egg connects with the larger organism that pulses unseen through leaf litter, crawls under the bark of dying trees, and connects with the roots of healthier ones. This is the feeding phase of the organism's life, or life cycle, and grows as masses of filamentous cells called hyphae. Only when these hyphae have gathered a sufficient harvest of food, and when the subterranean fungus is fattened and pumped full of water, can it surface to disturb our composure.

Biologists decipher the shape and structure of different organisms by thinking about the functions for which they may be adapted, or the challenges that have been overcome by developing in a particular way. The apparently ornamental figure of the phallic mushroom is really a very conservative structure. The top of the shaft is a sensible location for the spore mass because its pungent slime is concentrated where it acts best as a beacon to flies. Stinkhorn receptacles are very delicate structures. They are built

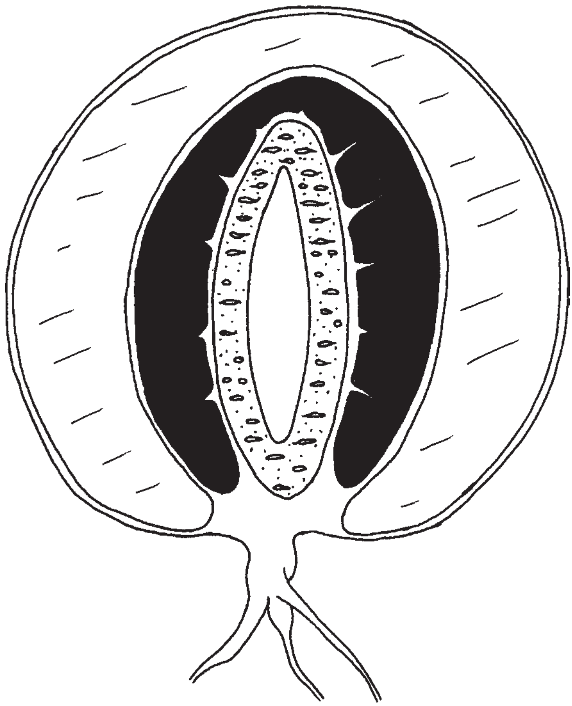

Fig. 1.3 Cut egg of phallic mushroom. The central receptacle, which expands to form the stalk, is surrounded by the green-black mass of developing spores called the gleba. Jelly surrounds the gleba.

from masses of corrugated hyphae that are stretched into a weft of filaments when the egg hatches. Most of the volume of the erect fruiting body is air. But mechanically speaking, the stinkhorn is comparable with the mammalian penis because both erections are maintained by pressurized fluid rather than a column of solid tissue. The penis contains flattened reservoirs that become engorged with blood, while the tissue of the stinkhorn receptacle is built to tear apart to make a honeycomb supported by pressurized water within its hyphae. Despite these similarities, the origin of the pressurized fluid is fundamentally different in the two structures. Penile blood pressure is generated by muscular activity; stinkhorn pressure is osmotic in origin, something akin to the way that water is soaked up into a dry sponge. While we can deconstruct the stinkhorn and explain its parts, the extraordinary phallic resemblance remains a great surprise. I suppose that this unusual fruiting body may be a jest by Satan—in its various stages of development, *Phallus* has been identified as the devil's eggs, devil's horn, and devil's stinkpot[2]—but I'm putting my money on the Darwinian explanation. At least for the fungus, fruiting bodies function to produce and disperse spores, nothing else.

Mycologists have described thirty truly phallic-looking mushroom species. As its common name suggests, the dog stinkhorn, *Mutinus caninus,* is smaller in stature, has a pink shaft, and lacks the bulbous head. It still smells awful and attracts flies. Species of *Dictyophora* are recognized by a lacy veil that hangs down as a skirt beneath the head (see jacket photo). The crinoline feminizes the phallic effect a little, and may offer a ladder that allows wingless insects to reach the spores by crawling from surrounding plants. The eggs of one species of *Dictyophora* are sold as delicacies in China and are also marketed as aphrodisiacs. Inside the egg, stinkhorn slime does not smell too awful, and some authors of mushroom guidebooks claim that the whole thing can be consumed without much suffering. In his book, *In the Company of Mushrooms*, Elio Schaechter[3] admitted to enjoying stinkhorn eggs and remarked that once filled with cream, rings cut from the expanded receptacles were delicious. On a more general note, it is a tragedy in a country as populous as China that anything from tiger turds to whale afterbirths can be sold as long as the suggestion is made that their consumption enhances erectile function.

The related cage fungi produce other kinds of flamboyant fruiting bodies that share the seductive power that phallic mushrooms wield over insects. Again, a preformed receptacle is packaged into an egg, and as this structure absorbs water and expands, it carries a stinking spore mass into the air. Rather than exiting the egg as a single shaft, the receptacles of cage fungi unfold into more open structures. *Clathrus* forms a spherical cage with spores spread on the inside of its bars (Figure 1.4 a). The receptacle of *Anthurus* separates into four or more arms that curl back over the egg to create a star (Figure 1.4 b). The arms are bright orange and their inner surface is smeared with the spores. A time-lapse video that shows the hatching of an *Anthurus* egg is quite shocking. It is difficult to describe the performance delivered by this fungus. There is nothing comparable. Here's my best shot: as this fruiting body issues from the ground, its livid arms simulate the agonized contortions of a horribly injured lobster. Other cage fungi form stalks with chambered heads or claws at their summit, and *Laternea* elaborates long arms like *Anthurus* but fuses them at their tips and dangles a reeking lantern inside the resulting vault (Figure 1.4 c). Flies are the usual vectors for spore dispersal, but ants and stingless bees have also been seen feeding on some cages.

Ileodictyon (intestinal net) is a cage fungus that grows in New Zealand and Australia. The Maori were quite taken with this fruiting body, according it nine different names and barbecuing its eggs. When it escapes human consumption, the white *Ileodictyon* cage expands from a buried egg and disengages from its papery skin. The detached cage, smeared with the usual excremental spore gunk, is then blown about on the surrounding grass. The Maori didn't eat the repugnant hatchlings, denigrating them as the "feces of ghosts or of the stars." The quote is taken from an intriguing article by the distinguished British mycologist Graham Gooday (a delightful scientist whose appearance evokes the stereotypical image of a Royal Air Force fighter pilot from the Second World War) and his friend John Zerning.[4] Zerning was struck by the shape of a dried specimen of *Ileodictyon* displayed by Gooday at a meeting. He noticed the resemblance between the cage and the geodesic homes designed by Richard Buckminster Fuller (Bucky), which became popular in the 1960s. This polyhedral form is also characteristic of the carbon-based molecules called buckminsterfullerenes, or buckyballs, which come close to making organic chemistry seem interesting. The similarity of hippy dwellings, buckyballs, and ghost feces is a reflection of the surprising strength offered by their lightweight polyhedral structure. Any weight saving is valuable for a fungus that, by necessity, makes conservative use of building materials. The resistance to compression of the *Ileodictyon* cage is important during its emergence from buried eggs and also when it is blown around. By maintaining an open shape, the receptacle provides a large surface area for exposure of the spores and their fetid scent.

Small changes in the details of receptacle development probably account for the great variety of mature fruiting body shapes in stinkhorns and cage fungi. For example, weakening of tissue along four or five tracks running the length of the receptacle would cause the shaft to split like a banana skin into four or five arms upon pressurized expansion. This would require alterations in the arrangement of the receptacle tissues inside the egg, or changes in the activity of specific enzymes during hatching. Then, with the mobilization of some genes to control the orange coloration of the receptacle, a *Phallus*-type fruiting body would be transformed into *Anthurus*.

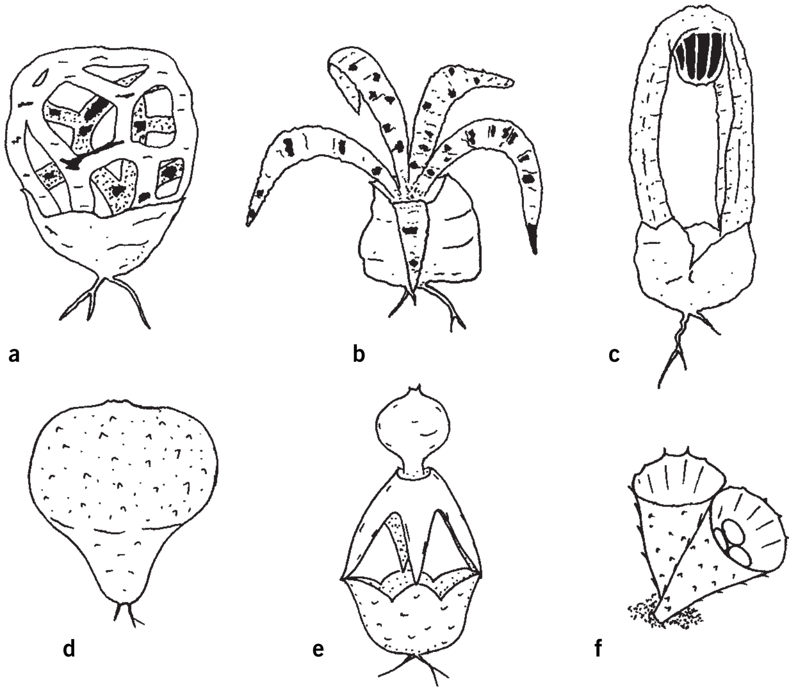

Fig. 1.4 Fruiting bodies of various gasteromycete fungi. (a–c) cage fungi: (a) *Clathrus ruber*; (b) *Anthurus archeri*; (c) *Laternea triscapa*; (d) puffball, *Lycoperdon perlatum*; (e) earth-star, *Geastrum fornicatum*; (f) bird's nest fungus, *Cyathus striatus*. Not drawn to the same scale.

This is an oversimplification of the developmental differences between these organisms, because there are other microscopic distinctions between their structures. But research on other fungi does suggest that conspicuous modifications in fruiting body morphology can be derived by surprisingly minor changes in the expression of enzymes during development.

Given the similarities among all of the phallic and cage fungi, it seems probable that natural selection may have sculpted the existing species in a relatively short period of time, perhaps in as little as a few million years. But why did all these structures evolve? Why did a phallus that divides at its tip evolve from an ancestor that did not, or vice versa? The answer surely lies in the relationships between these fungi and the insects and other invertebrates that disperse their spores. Different species of flies are lured by particular scents and personalized visual cues, so the various receptacles probably reflect distinctive solutions to the challenge of supporting and advertising spore slime. Biologists already recognize the significance of analogous characteristics in the origins of flowers among insect-pollinated plants. While humans are seduced by many floral perfumes, colors, and shapes, there are also numerous insect-pollinated flowers, such as the Sumatran giant *Amorphophallus titanum*, or corpse flower, which emit stinkhorny smells.[5] Stinkhorns, cage fungi, and putrid flowers have all evolved parallel features that attract insects that ordinarily congregate around carrion.

Along with the stinkhorns and cage fungi, other organisms including puffballs, earth-balls, earth-stars, and bird's nest fungi belong to the gasteromycete section of the basidiospore-producing fungi (Figure 1.4 d–f). Surpassing the inventions of all other fungi, the gasteromycetes have evolved a circus of mechanisms for dispersing their spores. Adapting an image from Richard Dawkins, baby stinkhorns use insect wings to fly away from their parents.[6] The offspring of puffballs, earth-balls, and earth-stars are puffed into the air and are then carried away by wind. Bird's nest fungi also use a two-stage dispersal mechanism. Their tiny fruiting bodies are shaped like champagne flutes and contain packets of spores called peridioles. Raindrops splash the peridioles from these cups onto surrounding blades of grass. Unsuccessful spores, those destined for a swift passage to stinkhorn heaven or hell, wait, and wait longer, and dehydrate, and die. Fortunate ones are consumed by herbivores grazing around the fruiting bodies, are carried by the animals as they pass through their digestive systems, and later deposited in a convenient pat of warm manure. Cow feces offer perfect residence for a young bird's nest fungus (suggesting that stinkhorn hell lacks the excrement-filled ditch of Dante's *Inferno*). Finally, one gasteromycete fungus shoots a black ball of spores from a fruiting body that operates as a tiny trampoline. This organism, called *Sphaerobolus*, grows on wood mulch, and can ruin the paintwork of a car parked close to a wet flower bed. The spore balls stick to smooth surfaces with incredible tenacity, and even when they are removed by vigorous cleaning, spots remain in the paint. Like the bird's nest fungi, this villain is adapted for an excursion through a herbivore gut, but it doesn't help to know that the intended targets of *Sphaerobolus* are grass blades rather than my beloved Ford Probe.

The gasteromycetes are defined by the fact that their spores form inside the fruiting body rather than on gills or other fertile surfaces exposed to the air. Their scientific name refers to this developmental feature: gastero = stomach, mycetes = fungi, stomach fungi. They seem to have evolved from different kinds of ancient fungi that produced conventional umbrella-shaped mushrooms, and as such are regarded as a ragbag of species rather than a natural grouping of organisms. The natural group is an important concept in biology. Contrary to the delusions of Christian fundamentalists, all animals with nipples and fur, for example, are descendants of a single ancestral species. They belong to a natural group, the mammals, from which every other living thing is excluded: without nipples you don't even merit an interview. Time is a crucial consideration in this discussion, because, of course, every pair of species shares an ancestor that could be found by delving back far enough into their respective evolutionary histories. Humans and stinkhorns are certainly related, and far more closely (according to their genes) than either is to any plant. But the natural group that includes *Homo* and *Phallus* also encompasses every animal and every fungus, and as such is a pretty esoteric gathering.

In common with stinkhorns, gilled mushrooms are devices for spore production and dispersal, nothing more or less. They have always held great fascination for me, and I suppose my deepest professional roots lie in childhood tales involving mushrooms. My earliest memory of a mycological experience comes from a dentist's office. I was 5 years old and under gas for multiple tooth extractions when I hallucinated a fairy ring with elves and other phantasms dancing around the mushrooms. Then I awoke, tumbling down the stairs from the torture chamber, bloody handkerchief pressed to my mouth. I have remained captivated by the eeriness of mushrooms, and have joined the ranks of mycologists who have become fascinated by trying to understand how they operate. This is not a simple matter.

Umbrella- and bracket-shaped mushrooms maximize their spore-producing capacity for a minimal investment in fruiting body tissue by supporting massive numbers of spores with a single stalk. These fungi spread their fertile tissues underneath the cap, folding a vast spore-producing mat called the hymenium over the surface of gills, ripples, or spines, or inside tubes. If a thin slice is cut from a mushroom cap with a razor blade and viewed under a microscope, spore-producing cells called basidia appear as projections from the hymenium (Figure 1.5). Basidia are four-pronged crowns shaped like miniature cow udders and bear a single basidiospore on each spike (or teat). One after the other,