Kingdom EUMYCOTA
Phylum 3: DIKARYOMYCOTA
Subphylum 2 — Basidiomycotina: the Basidiomycetes

Introduction

With the Ascomycetes under your belt, you should now find it easier to cope with the other half of Phylum Dikaryomycota. Subphylum Basidiomycotina has many important features in common with the Ascomycotina: (1) haploid nuclei in somatic hyphae; (2) chitinous hyphal walls; (3) regularly septate hyphae; (4) presence of central pores piercing the septa; (5) the potential for somatic, assimilative hyphae to anastomose; (6) the production of complex and often macroscopic sexual fruit bodies; (7) the presence of a dikaryophase in the life cycle (except in some anamorphic holomorphs); (8) a specialized mechanism for launching the meiospores into the air; (9) production of a conidial anamorph by many species. Make no mistake, ascomycetes and basidiomycetes evolved from a common stock.

Yet they are usually relatively easy to tell apart, macroscopically, microscopically and ultrastructurally, because it is probably a long time, even in geological terms, since they evolved apart. So we can expect to find a lot of differences as well. Here are some of them.

A) Walls: The walls of ascomycete hyphae are basically two-layered, those of basidiomycete hyphae are multi-layered. Don’t worry about this, because it can be determined only with the transmission electron microscope.

B) Septa (cross-walls): Dikaryomycotan hyphae are regularly septate, but the structure of the septal pore in different classes of the two Subphyla differs, as you can see in Fig. 5.1. The differences are important, but can usually be seen only with the electron microscope. Ascomycete septa (Fig. 5.1 A) are pierced by a simple, central pore, with a round Woronin body hovering on each side, ready to plug the pore if the hypha is damaged. Septa of class Saccharomycetes (many yeasts and related fungi that form ascus-like meiosporangia; see chapter 6), are often perforated by many micropores (Fig. 5.1 B). In classes Holobasidiomycetes (mushrooms, bracket fungi, etc.) and Phragmobasidiomycetes (jelly fungi) the septa have a central barrel-shaped structure called a dolipore covered on both sides by a cap of membrane called a parenthesome (Fig. 5.1 C). The septal pore of the rust fungi (atypical basidiomycotina placed in class Teliomycetes), is simpler, but is...
often blocked by a **pulleywheel occlusion** (Fig. 5.1 D). Both basidiomycotan pore mechanisms seem to prevent the migration of nuclei from cell to cell: the importance of this will soon become clear – read on.

C) The **Dikaryophase**. In ascomycetes, anastomosis of somatic hyphae may establish a heterokaryon (a hypha containing more than one kind of nucleus), but doesn’t usually initiate the dikaryophase. This is restricted to the special system of ascogenous hyphae arising from the ascogonium within the ascoma. But when monokaryotic basidiomycete hyphae anastomose, they may, if they are of compatible mating types, be establishing the dikaryophase, which can then grow for months or years before indulging in any overtly sexual behaviour. To put it in a nutshell: ascomycetous teleomorphs have a **restricted dikaryophase**, basidiomycetes often have an **extended dikaryophase**, and even their anamorphs can be dikaryotic, a phenomenon not found among the ascomycetes.

D) **Clamp connections**. In both groups the dikaryophase comes to an end in the hymenium of the teleomorph. In many ascomycetes, at this point, each ascogenous hypha develops a reflexed tip called a crozier, which allows the two nuclei of the dikaryon to

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**Fig. 5.1 Types of septa typical of various fungal groups.**
divide simultaneously, one in the hypha, one in the hook of the **crozier**, in such a way that the subsequently delimited ascus mother cell comes to contain a compatible pair of nuclei (Fig. 5.2 A). In ascomycetes, this phenomenon is generally restricted to the hymenium, but in many basidiomycetes, similar bypasses are found, not just at the base of the basidium, but at every septum in the dikaryophase. In basidiomycetes, they are called **clamp connections**, and their development is shown in Fig. 5.2 B. If a septate, somatic hypha has regular clamp connections, like those in the phase contrast picture (above, right) it must be that of a dikaryotic basidiomycete. If clamps are absent, the hyphae could still be those of a dikaryotic basidiomycete (many of the mushrooms called boletes have no clamps on their hyphae), but they could equally be those of a monokaryotic basidiomycete, or of an ascomycete, or even those of a zygomycete, since members of the Order Kickxellales have regularly septate hyphae.

E) **Basidia.** This is perhaps the most basic difference and one of the easiest to see. While the meiospores of ascomycetes are developed inside meiosporangia called asci (Fig. 5.2 A, Fig. 4.3), those of basidiomycetes are formed outside specialized meiosporangia called **basidia** (Fig. 5.2 B). Nuclear fusion and the subsequent meiosis happen inside the cell, but the spores blow out like tiny balloons at the ends of four tiny tapered outgrowths called **sterigmata**.

In most basidiomycetes, these spores are then actively expelled from their perches (Fig 5.3). But remember that just as in the ascomycetes, there is a significant minority of basidiomycetes which develop basidia, but have lost the spore-shooting mechanism. These we call **sequestrate**, because the mature basidiospores are kept inside the basidioma (which may simply remain closed, or may develop underground), being released later in a variety of ways, some of which involve animal vectors, as we shall see.

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**Fig. 5.2 Comparison of ascus and basidium development (see text).**
You may be relieved to learn that you don’t have to search for any of these microscopic and submicroscopic features to recognize a basidiomycete when you see one. The reason for that is that many diagnostic features are visible to the naked eye. What else do you know that looks like a mushroom? It is unique. The same is true of most other basidiomycete fructifications. You come to recognize certain basidiomycete mycelia on sight after a while, without even using a hand lens, because they tend to form delicate but visible fan-like arrangements on decaying wood. If you already recognize mushrooms, bracket fungi, puffballs, earth-stars, bird’s-nest fungi and stinkhorns, you’re well on the way to being able to tell almost any basidiomycete from an ascomycete (and from any other fungus).

I recognize three classes within the Subphylum Basidiomycotina. These are the Holobasidiomycetes, the Phragmobasidiomycetes, and the Teliomycetes. The first class includes all the common names just mentioned. The second includes many jelly fungi, and the third comprises the rust and smut fungi. We’ll visit them in turn.

Class Holobasidiomycetes

All basidiomycetes with holobasidia – those that are not subdivided by septa – belong here. This is the kind of basidium illustrated above, because it is the kind found in most basidiomycetes. Again, the presence or absence of cross-walls is a microscopic character that is often difficult to see. And again, there are macroscopic features that enable us to recognize 99% of all holobasidiomycetes as belonging to this class. If you don’t have these features at your fingertips already, time spent looking at the various illustrations in this text, and at one of the beautifully illustrated field guides listed at the end of this chapter, will pay off handsomely when you go outdoors to look for these fungi. It’s not that holobasidiomycetes are all the same; in fact, they present a dazzling diversity of form and function. But while most holobasidiomycetes develop characteristic fleshy, corky or woody basidiomata, those of phragmobasidiomycetes (which have basidia subdivided by septa) are often gelatinous, and teliomycetes have nothing you could call a separate fruit body, merely forming pustules on their living hosts. And in teliomycetes, the basidia develop directly from a specialized resting spore called a teliospore.

The Holobasidiomycetes comprise two highly interrelated series, called Hymenomycetae and Gasteromycetae. Most Hymenomycetes shoot their basidiospores actively from hymenia that are exposed at maturity (Gasteromycetes do not). Basidiospores which are to be forcibly discharged (ballistospores) blow out at an angle to the fine sterigma that bears them: in other words they are asymmetrically mounted, or offset, as can be seen in Figs. 5.2 B, 5.4 B and 5.10. Just before discharge, a droplet of fluid, enclosed within a membrane, appears at one side of the spore base, and within seconds the spore is shot away. A minute quantity of mannitol and hexose sugars is secreted from a small area at the base of the spore, forming a hygroscopic spot on which water condenses from the saturated air surrounding the basidium. The droplet then coalesces instantaneously with a film of water on the surface of the spore, as in Fig. 5.3, causing a rapid displacement of the spore’s centre of gravity. This redistribution of mass is opposed by the sterigma which is under high turgor pressure. As a result, the spore immediately breaks its fragile connection with the sterigma and shoots away with very high initial acceleration, though it doesn’t go very far. The mechanism has been described as a surface tension catapult. It is fascinating that essentially the same mechanism is found in the basidia of mushrooms, jelly fungi, rust fungi and some yeasts. It is a strong argument for the monophyly of the Basidiomycetes.

If you want to follow the extended trail of experiment and observation that led to the current explanation, I recommend that you read Money, N.P. (1998) ‘More g’s than the
Space Shuttle: ballistospore discharge. *Mycologia* 90: 547-558. There is also new evidence that some mushrooms chill their fruit bodies by evaporative cooling. This enhances condensation on their spores, which apparently need a layer of free water if the shooting mechanism just described is to work [see Husher et al. (1999) 'Evaporative cooling of mushrooms' *Mycologia* 91: 351-352].

Gasteromycetes, if they have hymenia, don't expose them when the spores are mature; the spores are symmetrically placed on the sterigmata, and are never actively shot away. I believe that the basidium originally evolved as a spore-shooting mechanism, but that for various ecological reasons, which we will explore, it has on many separate occasions lost that function. So our assumption is that the various kinds of gasteromycete have emerged independently, on many occasions, from among the Holobasidiomycetes. Oberwinkler, an authority on the classification of the Basidiomycetes, has recognized nineteen Orders of Holobasidiomycetes, but I will discuss only ten (and give a key to them later). Why the difference? He subdivides what I call the Order Aphyllophorales (bracket fungi and relatives) into six Orders, what I call the Agaricales (mushrooms) into three, and recognizes one or two obscure Orders I did not feel it essential to enumerate here (Only if you become a professional mycologist will you have to think about the possibility that there may indeed be nineteen Orders of Holobasidiomycetes!) First, two 'outlier' or atypical Orders.

1) **Order Exobasidiales**: 10 genera, 67 species. This Order is atypical in much the same way that the Taphrinales was atypical of the ascomycetes. Unlike most other holobasidiomycetes, *Exobasidium* doesn't produce a fruit body (a basidioma) – just a whitish layer of basidia on the surface of the host plant. The host in this case is a member of the Ericaceae. Other Exobasidiales occur on members of the family Commelinaceae. *Exobasidium* produces symptoms like those caused by the Taphrinales – excessive growth of the leaf tissues, and disturbances in photosynthesis that often cause the leaves to turn red. This has led to speculation that these two Orders represent some kind of connection between the subphyla.

2) **Order Dacrymycetales**: 11 genera, 72 species. These are all 'jelly fungi,' again atypical of the class, that grow on rotting wood. Their gelatinous, yellow basidiomata are common and conspicuous in wet weather, but shrivel up and almost disappear in dry periods. The basidiomata of *Dacrymyces* are irregular to the point of shapelessness, and look like those of some Phragmobasidiomycetes (the real jelly fungi) – a quick look at the basidia (Fig. 5.4 B) will settle the issue. Basidia of Phragmobasidiomycetes are septate, but dacrymycetalean basidia are not. They have a unique appearance: we call them tun-

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**Fig 5.3.** Current explanation of basidiospore discharge mechanism, from N.P. Money, 1998.
ing fork basidia because they develop two long arms that grow up to the surface of the jelly, where their basidiospores are produced and shot away. The basidiospores are also unusual in becoming multiseptate (phragmoseptate) after liberation. The gelatinous fruit body of *Dacrymyces* plays a double role in that it often produces an unnamed thalic-arthric conidial anamorph (Fig. 5.4 A) before the basidia develop. The basidioma of *Guepiniopsis* is more shapely than *Dacrymyces*, and a translucent gold in colour. On the west coast it is common on rotting branches in fall.

(3) **Order Aphyllophorales**: 400 genera, 1,200 species. This is one of the larger and more poorly defined groups of hymenomycetes, and one of the most diverse. Its name can be translated as ‘without gills,’ and it seems to be designed as a catch-all for hymenomycetes that don’t fit into the fourth Order, the Agaricales, which houses the mushrooms with gills or fleshy tubes. So the Aphyllophorales currently embraces eight families with conspicuous but different basidiomata – the club and coral fungi, the tooth fungi, the chanterelles and the horn of plenty, the dry rot fungi, the paint fungi, the ‘split-gills,’ and the bracket fungi. Most are saprobic on wood, and while they do us the favour of scavenging on fallen branches or logs and recycling the nutrients in these, they are equally at home attacking either the structural timbers of our houses, if we allow these to become damp, or the wood and roots of living trees. A few are ectomycorrhizal (see chapter 17). This Order is almost certainly heterogeneous, and will eventually be split up.

a) **Family Corticiaceae**. The basidiomata are often effuse or **resupinate** (spread out), on the surface of decaying wood. The hymenium may be smooth, wrinkled or toothed, and the basidiospores are smooth in outline, colourless or pale, and non-amyloid.

The members of this family are sometimes called ‘paint fungi.’ The spread-out basidioma of *Aleurodiscus penicillatus* even has the cracks you associate with old paint. Remember that even though it looks simple, a paint fungus may have a complex internal structure. Its microscopic structure is often intricate. The basal tissue is usually composed of only one kind of hypha, and is thus described as **monomitic**, but in some taxa the fruit

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![Diagram of Dacrymycetales: Dacrymyces stillatus.](image-url)
bodies are dimitic, with thin-walled generative hyphae and thick-walled skeletal hyphae (Fig 5.6). The hymenium may also incorporate specialized accessory sterile hyphae (e.g. crystal-encrusted cystidia (Fig 5.5A) such as those in Amylostereum, which also has what is known as a 'thickening' hymenium that produces successive crops of basidia). These are fungi that richly repay microscopic study. Despite this, relatively few mycologists have tangled with them, though my mentor, Luella Weresub (whose memory I still treasure, though she died in 1979), was one of them.

Anamorphs of this group of fungi may be thallic-arthric conidia produced when clamped hyphae disarticulate at the septa, as in the Osteomorpha anamorph of Trechispora, or more specialized conidiophores producing blastic-sympodial conidia, as in the unnamed anamorph of Sistotrema (see Kendrick and Watling 1979).

b) Family Thelephoraceae. These are like the Corticiaceae in many ways, but most fruit on the ground rather than on wood. The basidioma may be resupinate (spread out) or fan-like or stalked, and the hymenium may be smooth, warty or toothed. The basidio-

Fig. 5.5 Representative Aphylophorales.
iospores are irregular in shape, ornamented, brown to colourless, and non-amyloid. The dark tissue gives a green reaction with KOH (10% aqueous potassium hydroxide). *Thelephora terrestris* (Fig. 5.5 B), with brown, fibrous, vase-shaped basidiomata and a smooth hymenium, often establishes mycorrhizal relationships with young conifers in tree nurseries (see chapter 17).

c) Family Clavariaceae. Club and coral fungi. Arising from the ground or from wood, the erect, beige, yellow, white or purple basidiomata may be unbranched and club-shaped, as in *Clavariadelphus* (Fig. 5.5 E), clustered, as in *Clavaria* and *Clavulinopsis*, or repeatedly branched and coralloid, as in *Ramaria* (Fig. 5.5 E). They are monomitic or dimitic. The hymenium covers the upper part of the basidiomata, and is not put out of action by repeated wetting, as those of most other hymenomycetes would be. Basidiospores are colourless, smooth, and non-amyloid.

d) Family Cantharellaceae. The basidiomata are monomitic (constructed from a single kind of hypha) and arise from the ground. They may be yellow, stalked and rather mushroom-like, as in *Cantharellus cibarius* (the ‘chanterelle’ or ‘pfifferlinge,’ Fig. 5.5 D), though the hymenium is thrown into thick, fleshy folds which only superficially resemble gills. The cap of the more delicate (but still edible) *Cantharellus tubaeformis* is umbilicate (that is, it has a central, navel-like depression). Basidiomata may also be large and highly convoluted, as in the edible *Sparassis*, the cauliflower fungus, which can actually be much larger than any cauliflower I’ve ever seen. The edible ‘horn of plenty,’ *Craterellus*, is often almost black, and has a rather smooth hymenium. *Gomphus* looks rather chanterelle-like, but is not edible. The basidiospores of the Cantharellaceae are smooth, colourless and non-amyloid.

e) Family Coniophoraceae. The monomitic basidiomata usually appear on wood, and the hymenium can be smooth, toothed, folded or tubulate. That of *Serpula lacrymans*, the dry rot fungus, is dimpled. The basidiospores are smooth, brown and double-walled. *Serpula* and *Coniophora* (the cellar fungus) cause serious rots of structural timbers, and *Serpula* can even grow through brick walls to find suitable substrate.

f) Family Hydnaceae. The tooth fungi (Fig 5.5 C). The hymenium covers tapering teeth that point vertically downward, like miniature stalactites. The basidiomata may be rather irregular and eccentric, as in *Hericium erinaceus* (the wood urchin, which fruits on the side of trees) and *Hericium coralloides*, or very mushroom-like, as in *Dentinum (Hydnum) repandum*, the edible ‘hedgehog mushroom’ or ‘sweet-tooth.’ *Auriscalpium vulgare*, a delicate member of the Hydnaceae with a long stipe and an eccentric cap, fruits on decaying Douglas fir cones. Many corky or woody species of *Hydnellum* grow on the forest floor, often developing around and engulfing conifer needles and twigs. *Sarcodon* is large, with a scaly cap and a dark stipe. The spores of this family are smooth, colourless, and non-amyloid.

g) Family Schizophyllaceae. The common (and therefore successful) *Schizophyllum commune* (Fig. 5.5 F), often seen on dead branches, looks like an agaric without a stalk, but is really a compound fructification, in which the inrolled edges of contiguous cupulate basidiomata give it its misleading common name, ‘split gill.’ This species is easily grown in culture, and is a popular subject for genetic research.

h) Family Polyporaceae. The bracket or shelf fungi. These are frequently divided up into several families by modern authors (see discussion of generic concepts, below). The basidiomata usually arise on wood, and may persist for several years. The underside of the fruit body is generally riddled with thousands of pores, the openings of vertical tubes which are lined with a basidial hymenium. Since the pores may be a couple of centimetres deep, this is a very efficient way of increasing hymenial area. Larger species with peren-
nial fruit bodies also add a new layer of tubes each year and may eventually become almost a metre across, so spore production may reach astronomical numbers.

*Bridgeoporus (Oxyporus) nobilissimus* is a rare and threatened species found only in old-growth forests of the Pacific Northwest. United States law now mandates that 240 hectares (600 acres) of forest must remain undisturbed around each known site of this fungus. Progress! A basidioma of this species was formerly noted in the *Guinness Book of Records* as the world’s largest fungal fruit body, but it has now been supplanted by a specimen of *Rigidoporus ulmarius* that is still growing actively at Kew, England. *Polyporus squamosus*, the Dryad’s saddle, is easily recognized by the conspicuous scales on the upper surface of its fruit body and its relatively soft texture. *Fomes fomentarius* has very tough, hoof-shaped basidiomata. A few polypores, such as *Laetiporus sulphureus*, which produces spectacular orange and yellow fruit bodies on fallen trees, are soft enough when young to be eaten (common name: Chicken-of-the-Woods), though they should be avoided if the substrate is *Eucalyptus*. *Albatrellus ovinus* is another unusual polypore which looks very like an agaric, grows on the ground, and has soft flesh. The pores are very narrow and shallow. *Heterobasidion annosum* is highly pathogenic to many conifers, and causes serious root-rots. I have seen a forest clearing produced by this fungus: it had killed representatives of fourteen different conifers, many of them introduced species. *Piptoporus betulinus*, on the other hand, kills only birch trees. *Trametes versicolor* (often called the turkey tail) is one of the smaller and most common saprobic polypores.

Like many other fungi, polypores often have anamorphs (see Kendrick and Watling 1979), though these may be very inconspicuous. *Heterobasidion annosum* has a hyphomycetous anamorph in the genus *Spiniger*, which forms many conidia synchronously on an apical vesicle. The *Psychogaster* anamorph of *Trametes* forms alternate-artric conidia (to review conidium development, return to chapter 4).

Many polypores, e.g. *Poria*, *Polyporus*, and *Ganoderma*, may not kill trees, but they cause serious decays of both standing and structural timber. These rots cost us many millions of dollars every year. The general division here is into brown rots, where only the cellulose is digested, and white rots, where both cellulose and lignin are metabolized. *Coltricia cinnamomea*, a centrally stalked, ground-fruting polypore, is atypical in being ectomycorrhizal (see chapter 17)

The generic concepts among the polypores have changed a lot in recent years as a result of extensive anatomical and enzymological research, and identification is rather difficult for the amateur. How do we define genera in the Polyporaceae?

To the uninitiated, most polypores tend to appear rather similar – a bracket-shaped excrescence on a branch or trunk of a tree. Most of the bracket fungi were at one time put into the genus *Polyporus*. No more! Mycologists now recognize almost 100 genera of bracket fungi. Why has this plethora of names been introduced? It is because a lot of new microscopic and biochemical characters have been recognized (which certainly doesn’t make life easier for the student). These characteristics are as follows:

1. **The kind of hyphal system.** All fungal fruit bodies are built up of hyphae, but those of polypores can have as many as three different major kinds of interwoven hyphae, and are called monomitic, dimitic or trimitic, according to whether they have one, two or three major hyphal systems. Monomitic fruit bodies are made up of what we call generative hyphae, which are septate, can be thick- or thin-walled, and may or may not have clamps. Most such species are relatively soft in texture (e.g., the white cheese polypore, *Tyromyces chioneus*). Dimitic basidiomata have two hyphal systems, the generative being supplemented by either thick-walled, non-septate skeletal hyphae which give basidiomata a hard, tough texture (e.g., the artist’s conk, *Ganoderma applanatum*), or by thin-walled, highly branched binding hyphae (e.g., the sulphur shelf, *Laetiporus*).
Suillus sulphureus. Trimitic basidiomata are composed of generative hyphae, plus skeletal hyphae, plus binding hyphae (e.g., the turkey tail, Trametes versicolor) (Fig. 5.6 – after H.J. Hudson, Fungal Biology)

(2) The kinds of digestive or degradative enzymes produced by the fungus. Brown rot fungi digest cellulose but not lignin. White rot fungi digest lignin, but tend to leave some cellulose. Mycorrhizal fungi may not degrade wood at all.

(3) The septation of the generative hyphae. In some species they are simple septate, while in others they are regularly clamped.

(4) The kinds of cystidia produced, and their origin.

(5) The reaction of basidiospores with Melzer’s reagent (they are amyloid [stain blue] in Bondarzewia, dextrinoid [stain brown] in Perenniporia).

(6) The size, shape, ornamentation and walls of basidiospores (spores have a truncate base and a double wall in Ganoderma, are minutely spiny in Heterobasidion).

Perhaps the best keys available are to be found in the two-volume North American Polypores by Gilbertson and Ryvarden (1986, 1987; Fungiflora, Oslo), but many mush-
room field guides also contain relatively good coverage of polypores, and if you include these persistent fungi among your collections, you will come home with something interesting at any time of year – even in the depths of winter, or the driest month of summer.

**Agaricales and Gasteromycetes**

4) **Order Agaricales**: 300 genera, more than 10,000 species. This Order brings together the most familiar of all fungi, the so-called mushrooms and toadstools. Since no two people agree on the precise dividing line between these two categories, it is better to call them all **agarics**, the term used by the knowledgeable, among whom you should soon be numbered if you are receptive to the material in this section.

Compared to polypores, agarics are relatively ephemeral, the basidiomata persisting for anything from a few hours to a few weeks, depending on the species. They occur seasonally, fruiting mainly in late summer or fall, though on the west coast of North America they can be found in almost any month of the year. The Mycological Society of San Francisco holds its annual Mushroom Fair in December, when agarics are only memories in Minnesota and Manitoba.

Agaric fruit bodies arise from an extensive, perennial mycelium which ramifies, invisible to the eye, through soil, plant debris or wood, gathering energy for that once-a-year (or once-every-several-years) splurge. Some fairy rings (which are really enormous, radially extending fungal colonies) are estimated to be over 400 years old, and have presumably produced flushes of basidiomata in many of those years. A single colony of *Armillaria ostoyae* growing in the forests of western North America has been found to cover 600 hectares, and to have biomass exceeding that of a blue whale. Such colonies are probably at least 1,000 years old.

Most agarics are either **saprobic**, exploiting dead organic matter, or **ectomycorrhizal**, establishing mutualistic symbioses with the roots of woody plants, especially conifers of the economically important family Pinaceae. This explains why woodlands are often such excellent places to look for agarics. A detailed discussion of the ectomycorrhizal relationship is given in chapter 17. Only a few genera, such as *Armillaria*, are parasitic, and even that notorious genus (see Forest Pathology in chapter 12) is sometimes saprobic.

Most agarics share the same basic design (Fig. 5.7 A-D). There is a central, vertical stalk or **stipe**, with a horizontally spreading **cap** or **pileus** at the top. The underside of the cap usually bears delicate, radially arranged, vertical plates called **gills** or **lamellae**, though some have vertical fleshy tubes instead. The hymenium covers both sides of each gill, or lines each tube. Basidiospores are launched from the basidia, drop through the space between adjacent gills, and enter the more turbulent outside air which carries them away. In some genera, for example *Amanita*, the developing basidioma is totally enclosed within a membranous **universal veil**, remains of which can be seen on the mature, expanded agaric in the form of a sheath or **volva** around the base of the stipe, and spots, warts or patches on the cap. There may also be a **partial veil** connecting the stipe and the edge of the cap in young specimens, enclosing and protecting the developing gills. This, too, may remain on the stipe of the mature, expanded agaric as a membranous **ring** or **annulus** (as in *Amanita* and *Agaricus*), or as a filamentous, cobwebby veil or **cortina** (as in *Cortinarius*). A few agarics have both ring and volva; some others have only one of these features, and the majority have neither.

Agarics are complex, rather variable structures, and have many other taxonomically valuable features. The check-list given below includes many (though not nearly all) of them, and shows the kinds of information we need to collect in order to classify the thousands of different agarics. If you are going to make a serious stab at it, you could do...
worse than photocopy the chart on page 90-91 and fill in as many of the blanks as you can before going to the books, or to a mushroom identification software program such as Matchmaker.

If you try to find all of those characters in a number of agarics (admittedly a counsel of perfection), you will learn a tremendous amount about them. In fact, you can usually identify them to genus with a small fraction of those characters, though getting them to species will probably call for much more information. If you read what follows, in which I introduce you to representatives of sixteen families, you will see which of the characters mentioned above are the most important in separating them.

a) Family Agaricaceae. The genus *Agaricus* (Fig. 5.7 B), to which the supermarket mushroom belongs, (1) has a ring, (2) lacks a volva (that is, it has a partial veil but no universal veil), (3) its gills are not attached to the stipe (they are described as free), and (4) its spore print is dark. Other members of the family such as *Leucoagaricus* may have spore prints of different colours, but they are never rusty brown or cinnamon. *Leucoagaricus naucinus*, which is common on lawns, is an all-white or cream-coloured agaric with a ring, but no volva. It has an uncomfortable resemblance to the deadly poisonous *Amanita virosa*, so although it is not dangerous (edible to some, a gastric irritant to others), I always
CHARACTERISTICS FOR THE IDENTIFICATION OF AGARICS

Locality: ____________________________ Date:__________

Habitat notes:
soil type:__________________________
soil pH:________
vegetational community:__________________________

BASIDIOMATA:
solitary / in troops / in rings / on ground / on wood / on living tree/other
(describe)__________________________

(Photograph, draw or preferably paint general view and vertical section of fruit-body)

MACROSCOPIC CHARACTERS

CAP (PILEUS): Diameter: (range) __-__ cm
Shape: convex / bell-shaped / conical / umbonate / flat / depressed / umbilicate /
funnel-shaped/cylindrical (when young) _____ (when mature) _____
Surface colour: when immature ___________ when mature ___________
when wet ___________ when dry ___________
Surface texture (circle one or more): dry / moist/ greasy / viscid / glutinous / peeling
easily / smooth / matt / polished / irregularly roughened / downy / zoned / velvety /
scaly / splitting / shaggy / with volva fragments
Margin: (choose one or more) regular / wavy / upcurved / incurved / smooth / rough /
furrowed / striate / split / shaggy / with veil fragments

GILLS (or TUBES or TEETH):
(choose as appropriate) remote / free / adnate / adnexed / sinuate / decurrent /
crowded / distant / forked / anastomosing
Easily separable from the cap-tissue: Yes/No
thick / thin
consistency: brittle / pliable / fleshy / waxy
Colour: when immature ___________ at maturity ___________
Number of different gill lengths (series) __ or number of tube layers __
Obvious features of gill-edge, tube-edge, e.g., colour (esp. if different from rest, i.e.,
marginate); outline - smooth / jagged ___________

STIPE:
central / off-centre / absent / hollow / solid / stuffed (with cottony mycelium) /
tapering upward / equal (not tapering) / rooting
Dimensions: length (range) __-__ thickness __ -__
Colour: when immature ___________ at maturity ___________
Consistency: fleshy / stringy / brittle / cartilaginous (flexible) / leathery (tough) /
woody
Surface: fibrillose / dry / viscid / scaly / smooth
Characters of stipe base (e.g., swollen, rooting, etc.):____________________
CHARACTERISTICS FOR THE IDENTIFICATION OF AGARICS (cont’d)

VOLVA, if present: sheathing stem base / scurfy rings

RING, if present: single / double / membranous / filamentous / persistent / fugacious / moveable / thick / thin / apical / median / hanging (skirt-like)

FLESH: colour: inside cap: when wet ________ when dry ________
inside stipe: when wet ________ when dry ________
Colour changes when exposed to air: _______________________
Milk-like latex: present/absent
Colour when exuded ________ after exposure to air ________
Smell: before cutting ________ after cutting __________

MICROSCOPIC CHARACTERS

BASIDIOSPORES:
Colour: in mass (spore print) __________
Shape: spherical / ovoid / elongate / angular / curved: size range _-__ x _-__ μm
Ornamentation: none / warty / rounded / pointed (spiny) / ridged / striate / net-like
Size and shape of germ-pore, if present _______________________
Iodine reaction of spores: blue-black to dark violet (amyloid) / red-purple (dextrinoid) /
yellow-brown or brown (non-amyloid)

BASIDIA: length:width ratio — less than 4:1 / more than 5:1
number of sterigmata__

CAP TRAMA: types of cell present ___________________________

GILL-TISSUE (TRAMA): type and arrangement of cells between adjacent hymenial faces: divergent/parallel/convergent/interwoven
(These tramal characters are not easy to observe, but if gills are sandwiched between two microscope slides placed at right-angles to one another and sliced with a new razor blade, the resulting sections can be revealing.)

CAP-SURFACE (PILEIPELLIS): cells of outer layer: filamentous / rounded

SPECIALIZED STERILE CELLS — CYSTIDIA: present on: gill-face / gill-edge / cap / stipe
Shape: filiform / cylindrical / clavate / ventricose / branched (sketch here)
Size _-__ x _-__ μm
thick-walled / thin-walled / colourless / pigmented
other features __________________________
advise people against making a meal of it. *Lepiota clypeolaria* has a scaly cap and a ring, both typical of the genus. *Macrolepiota rachodes* is a much larger, edible species. Again, note the large cap scales and the conspicuous ring. This species was placed in *Lepiota* until recently. *Endoptychum* is a sequestrate derivative of *Agaricus*. The gill cavity never opens, and the gills themselves are convoluted and spongy – a totally inappropriate configuration for dropping spores into the air.

b) Family Amanitaceae. All members of the genus *Amanita* (Fig 5.7 A) have (1) white spore prints, and all have (2) a universal veil and (3) a partial veil. Most therefore have a ring and a volva at maturity, as in *Amanita calyptra*. However, these generalizations camouflage a lot of variability, especially in the volva. (4) The gill trama is divergent (Fig. 5.7 E), (5) the gills are often, but not always, free (not attached to the stipe). In some species, e.g., *Amanita muscaria*, at maturity the volva is reduced to scurfy rings around the base of the stipe. However, the upper part of the universal veil often breaks up into spots, warts or patches on the cap as the fruit body expands. These are an excellent clue to the prior existence of a universal veil, and are particularly obvious in *Amanita muscaria*. In *Amanita fulva* (formerly placed in the genus *Amanitopsis*) the ring is essentially absent. The volva is conspicuous, but splits cleanly and so does not leave patches on the cap.

Because some *Amanita* species are deadly poisonous (see chapter 22), the genus has even made the cover of ‘Scientific American,’ and mushroom hunters (especially those planning to eat what they collect) should always make sure they get to the base of the stipe of any agaric they pick, so they can see whether or not there’s a volva. The ‘destroying angel,’ *Amanita virosa*, is pure white, with ring, conspicuous volva and even a white spore print. But this species, like *A. fulva*, does not have spots (patches of universal veil) on the cap. Like most other members of the family, this lethal species (see chapter 22) is ectomycorrhizal, and so fruits only near tree species with which it is symbiotic (see chapter 17).

*Termitomyces*, a saprobic genus, is involved in another kind of mutualistic symbiosis: with mound-building termites in Africa and Asia, a relationship discussed in chapter 16. Its fruit bodies are also widely eaten – see chapter 18.

c) Family Bolbitiaceae. Basidiomata of the genus *Bolbitius* are small and ephemeral, since their tissues autolyze (self-digest) at maturity. (1) The surface layer of the cap (the pileipellis) is epithelial (the cells are swollen, and don’t appear filamentous). (2) The spore print is ochraceous to rusty brown, and (3) the spores have a germ pore. Representative genera are *Agrocybe*, *Bolbitius*, and *Conocybe*. *Conocybe filaris* contains deadly amatoxins (see chapter 22).

In addition to normal agaricoid species, the Bolbitiaceae has sequestrate members with basidia that don’t shoot their spores. The genus *Gastrocybe* still looks like an agaric, but its spores are symmetrically mounted, its cap does not open, and it has a habit of falling over as soon as it comes up. These features show that it is even now actively evolving, and that its spores are not wind-dispersed.

d) Family Coprinaceae. This family also has (1) a pileipellis of swollen cells, but (2) the basidiospores are usually black and smooth, and (3) have a germ pore. Members of the advanced genus *Coprinus* have weed-like vigour and opportunism, pioneering the exploitation of such habitats as recently disturbed ground and dung. The best-known species, *Coprinus comatus* (Fig. 5.6 C), the ‘shaggy mane’ or ‘shaggy ink cap,’ has a complex set of physical arrangements and a precisely timed sequence of events during spore liberation that make it one of the most advanced of all agarics. It is edible, but only when young, when the gills are still white. Later they turn red-brown, then black, and melt away from bottom to top. This behaviour is described in detail in chapter 8. *Coprinus atramentarius*
is another edible species, but it must not be washed down with alcohol. The reason for this prohibition is explained in chapter 22.

_Coprinus plicatilis_ is one of many small, delicate species, some of which grow specifically on dung. More details about fungi that specialize in exploiting this substrate can be found in chapter 11. I have seen a sequestrate member of this family, _Podaxis_, fruiting in deserts on three continents. It looks very like _Coprinus comatus_, with black spores; but it has no recognizable gills and doesn’t autolyze. The spore mass is dry and disperses only when the fruit body disintegrates. Though some taxonomists erected a special Gasteromycete Order for _Podaxis_ and similar fungi, I treat it as a sequestrate member of the Coprinaceae, with an appropriate common name ‘the desert shaggy mane.’ It simplifies life to do this, and I believe it also emphasizes the true relationships of these fungi.

e) Family Cortinariaceae. Here (1) the cells of the pileipellis are filamentous, never swollen, and (2) the basidiospores are rusty brown and often (3) rough-walled. _Cortinarius, Galerina, Gymnopilus, Hebeloma, Inocybe_ and _Rozites_ are representative genera. The best known genus is _Cortinarius_, often easily recognized at the generic level by its unusual partial veil, which is called a _cortina_ (curtain) – numerous individual filaments stretch between the stipe and the edge of the pileus as it expands. After the cortina ruptures, the filaments can often be seen on the stipe, usually coloured brown by spores that have fallen on them. _Cortinarius_ is a very large and diverse genus, with perhaps 2,000 species, most or all of which are ectomycorrhizal. Identification to species is usually almost impossible, because the necessary monographs have not yet been published. In fact, _Cortinarius_ is so large and unwieldy that it is now generally subdivided into seven groups, more or less as follows:

(1) Members of Subgenus _Cortinarius_ have warty spores, cystidia, and the fruit bodies are often saturated with a purple pigment that is different from the pigments found in the other groups. Only a few species are now placed here, but these include the well-known _Cortinarius violaceus_.

(2) Members of Subgenus _Myxacium_ have a slimy cap and a slimy stipe.

(3) Members of Subgenus _Phlegmacium_ have a slimy cap, a dry stipe and a bulbous base.

(4) Members of Subgenus _Telamonia_ have a dry, hygrophanous cap, and the cap tissue blackens in KOH.

(5) Members of Subgenus _Leprocye_ have a dry, non-hygrophanous cap, and lack anthraquinone pigments. All deadly poisonous _cortinarii_ are members of this subgenus.

(6) Members of Subgenus _Dermocybe_ have dry caps, and are saturated with water-soluble anthraquinone pigments – the gills are especially brightly pigmented.

(7) Members of Subgenus _Sericeocybe_ have dry caps with a silky surface, and are non-hygrophanous. They are often difficult to separate from the _Telamonias_.

Some species of _Cortinarius_ subgenus _Leprocye_ are insidiously poisonous because they contain the toxin orellanine. You can read the rather horrible details in chapter 22. Many _Hebeloma_ species are ectomycorrhizal. _Galerina autumnalis_ is a small but deadly poisonous, amatoxin-containing species that grows on rotten wood in North America. Most species of the ectomycorrhizal _Inocybe_ are also poisonous because they contain muscarine, and _Gymnopilus spectabilis_ sometimes contains the hallucinogen _psilocybin_ (see chapter 22). But at least one member of the Cortinariaceae, _Rozites caperata_, is a well-known and highly regarded edible (see chapter 18). _Crepidotus_ is atypical; it is one of a fairly small number of asymmetrical or fan-shaped agarics in which the cap is laterally attached to the substrate and has little or no stipe.
Some members of the Cortinariaceae have become sequestrate. The genus *Thaxterogaster* closely resembles *Cortinarius* in many ways, but its cap never expands, and its gills have become so convoluted that even if they were to be exposed, they could not successfully drop many spores into the air. I have often found a beautiful purple species of *Thaxterogaster* in the Southern beech (*Nothofagus*) forests of New Zealand. A brown species of *Thaxterogaster* that I also found in New Zealand had even lost its external stipe, and looked rather like a puffball, though a vertical section of the fruit body revealed a central column of stipe tissue — the transformation still isn’t complete. The stalked, brown-capped *Thaxterogaster pingue* occurs in western North America. *Hymenogaster* is another sequestrate derivative of the Cortinariaceae.

f) Family Entolomataceae. (1) The spore print is pink to salmon-coloured, and (2) individual spores are extremely angular or sometimes longitudinally ridged; (3) the gills are attached to the stipe. *Eniiloma, Nolanea, Leptonia* and *Clitopilus* are representative genera of this mainly terrestrial (ground-fruiting) family. Most species of the mycorrhizal genus *Entoloma* contain gastro-intestinal irritants, and some can cause serious poisoning. *Entoloma abortivum* is a common species in which normal fruit bodies are often accompanied by lumpy, rounded, misshapen ones. We now know that the latter are being attacked by another agaric, *Armillaria mellea* (Tricholomataceae), whose basidia can be found in them. The easily recognized parasitized basidiomata are edible. *Entoloma* has given rise to a sequestrate offshoot, *Richoniella*, whose basidiospores are angular, exactly like those of *Entoloma*, and unerringly reveal the evolutionary origin of this sequestrate form.

g) Family Pluteaceae. (1) The spore print is pink, like that of the Entolomataceae, but (2) the spores are ellipsoidal and smooth, (3) the gills are free (not attached to the stipe), and (4) the gill tissue or trama is convergent. The lignicolous (wood-inhabiting) genus *Pluteus* has 100 species, of which *Pluteus cervinus* may be the most common. Perhaps the easiest way to make an unequivocal identification of this species is to squash a tiny piece of a gill under a coverslip on a 3 × 1" glass slide, and examine it under a microscope. This should reveal what we call ‘comute cystidia,’ large cells bearing apical horn-like projections that are unique to the gills of *Pluteus cervinus*. They are one of the excellent reasons that those studying mushrooms should get hold of a microscope if at all possible: it can sometimes make identification really easy.

*Volvariella volvacea*, the straw mushroom, though not native to North America, is the best-known member of the genus, since it is widely cultivated in the Far East (see chapter 18). Next time you eat mushrooms at a Chinese restaurant, see if they belong to this species — you can easily spot the persistent volva almost enclosing the whole basidioma. I got some living specimens of this fungus from a mushroom grower in Java, and later watched them open and make a profuse pink spore print.

h) Family Hygrophoraceae. (1) The basidia are long, (2) the spore print is white, and (3) the gill trama is divergent or parallel. Species of *Hygrocybe*, the most common and conspicuous genus, have parallel gill trama (Fig. 5.7F), are usually yellow, orange or red, and have a very characteristic waxy, translucent appearance. Species of *Hygrophorus*, the other genus of the family, have divergent gill trama (Fig. 5.7E), often have a partial veil, and are white, grey or brown. (Divergent gill trama = *Hygrophorus*, parallel gill trama = *Hygrocybe*).

i) Family Strophariaceae. A saprobic family that contains many ‘magic’ mushrooms. (1) The spores are purple-black or brown, (2) are smooth-walled and (3) have a germ pore; (4) the pileipellis is filamentous; (5) the gills are attached to the stipe and (5) often bear accessory cells called chrysocystidia, which have contents that stain yellow in alkali.
Some species of *Psilocybe* (e.g., *P. cubense*) and *Stropharia* contain the hallucinogen *psilocybin*, and the flesh of such species often turns blue when bruised. It is easy to grow *Psilocybe cubense* in culture, but for some peculiar reason possession of psilocybin-containing species is illegal. This topic is explored further in chapter 22. The non-hallucinogenic genera *Pholiota* and *Hypholoma* usually fruit on wood. Sequestrate derivatives of the Strophariaceae found in New Zealand and Australia are placed in the genus *Weraroa*.

j) Family Tricholomataceae. This is the largest and most diverse family of agarics, with over 75 genera. It is not a 'natural' family, and is now in the process of being subdivided, so we can make only a few generalizations about it. (1) The spores are white to pink in mass, and (2) have no germ pore; (3) the gill trama is parallel, and (4) the gills are attached to the stipe. Not a particularly encouraging way to define a family.

A variety of genera are mentioned below in alphabetic order:

*Armillaria mellea*, the so-called honey mushroom, can be a dangerous tree pathogen, though what used to be thought of as a single species is now known to comprise several distinct taxa — for example, the common *Armillaria* of the west coast of North America is *Armillaria ostoyae*, one genet of which extends over 600 hectares.

*Armillaria mellea* produces characteristic blackish mycelial strands called rhizomorphs under the bark of affected trees. *Cantharellula umbonata* has unusual but highly characteristic forking gills. *Catathelasma* is a genus of large mycorrhizal agarics with a conspicuous and persistent ring. This genus resembles the much-sought-after pine mushroom (*Tricholoma magnivelare*) but lacks its penetrating spicy odour, and is not regarded as edible. *Clitocybe clavipes* has decurrent gills and a swollen stipe base. *Clitocybe dealbata* contains the toxin *muscarine* (see chapter 22). *Collybia* has a somewhat confused generic concept. The basidiomata of the type species and a few other species are very small and arise from sclerotia, as in *Collybia cookei*, which grows on dead agarics, and *Collybia tuberosa*, whose sclerotia resemble apple seeds. *Collybia racemosa*, another small species, produces a most unusual *Sclerostilbum* synnematal anamorph along the stipe which sometimes forgets to develop a cap. Larger species, such as *Collybia maculata*, have diagnostic brown-staining propensities, but such species are now being moved to other genera. A good web site dealing with this genus is:


*Flammulina velutipes*, the ‘velvet stalk,’ is a wood-inhabiting species that often fruits in winter. It is also grown in cultivation, and etiolated basidiomata with tiny caps are marketed as ‘enoki-take’ (see chapter 18). *Laccaria laccata* is a very common mycorrhizal agaric which has unusual globose or ellipsoidal, spiny, amyloid basidiospores. There is an excellent on-line key to species of *Laccaria* at:

http://www.fmnh.org/candr/botany/botany_sites/fungi/index.html

*Lepista nuda* is a common species which is also a choice edible, despite its rather unappetizing lilac to purplish colour. *Lyophyllum decastes* is widely eaten, but does not agree with some people. *Marasmius oreades* is the edible fairy ring mushroom commonly found in pastures. *Mycena leaiana* is an unusually large and brightly coloured representative of this saprobic genus which has marginate gills (the edges are a different colour from the rest of the gill). In this case the vivid orange colour at the edge of the gill is produced by a concentration of cystidia with orange contents. *Nyctalis asterophora* parasitizes *Lactarius*. Although the *Nyctalis* looks like a mushroom, its cap often becomes almost entirely converted into conidia, so it is effectively an anamorph. *Xeromphalina campanella* is a very small saprobic species that fruits profusely on decaying tree stumps. *Xerula radicata* (formerly *Collybia*, formerly *Oudemansiella*) represents a modern trend
to break up the Tricholomataceae into smaller families. It is placed in the recently-proposed family Xerulaceae. One of the mysteries attached to the Tricholomataceae is that despite the very large number of taxa it encompasses, only two sequestrate forms are known: *Hydnangium* and *Podohydangium*, both of which arose from *Laccaria*. Compare that with what happened in the next family, where sequestrate genera outnumber those that shoot their spores.

k) Family Russulaceae. An almost entirely ectomycorrhizal group, with flesh that is distinctively brittle due to the presence of groups of unique, turgid, spherical, thin-walled cells called **sphaerocysts**. Some taxonomists think these fungi are sufficiently different from other agarics to give them the rank of Order (Russulales).

The spores are also unique in having elaborate ornamentation of ridges and warts. This ornamentation, but not the rest of the spore wall, stains darkly (usually blue-black) in Melzer's reagent. This is known as the amyloid (or starch-like) reaction. The spore print of the Russulaceae is white, cream or yellow.

The family Russulaceae contains two large epigeous agaric genera, *Russula* and *Lactarius*, and six much less common sequestrate derivatives (which don’t shoot their spores, and so don’t give spore prints). Although *Russula* and *Lactarius* are similar in many respects, they are easily distinguished by the presence of a milky latex in *Lactarius* (‘milky caps’), and by the absence of latex and the bright colour of the pileus in most species of *Russula*. *Russula virescens* is widely eaten in China, though only *Russula xerampelina*, with its shrimp-like flavour, is widely eaten in North America.

A section through a species of the sequestrate *Macowanites* reveals a reduced stipe, and shows that the gills are distorted and clearly not the vertical plates of tissue seen in true Russulas. Nevertheless, the spores of *Macowanites* have amyloid ornamentation and are clearly russulaceous. *Russula* has given rise to two separate sequestrate lines, *Macowanites* - *Gymnomyces* and *Elasmomyces* - *Martellia*. Both involve an agaricoid and a hypogeous form, and both retain micro-anatomical characters, like sphaerocysts and amyloid spore ornamentation, that give surprising proof of their origin in *Russula*.

All species of *Lactarius* bleed some kind of latex when damaged, giving them their common name of milky-caps. The highly appropriate Latin name also conveys this message. The latex unequivocally separates *Lactarius* from *Russula*. *Lactarius deliciosus* bruises green, but has orange latex which oozes out when the basidioma is damaged. The latex in *Lactarius vinaceorufescens* is especially concentrated just above the gills, and although whitish when it emerges, becomes yellow after a few seconds.

From *Lactarius* have evolved two sequestrate genera: *Arcangeliella* (still mushroom-like [agaricoid], but with a cap that encloses the gills, and non-shooting basidia), and *Zelleromyces* (which has become hypogeous and truffle-like). All three genera produce latex.

1) Family Boletaceae. Some mycologists consider this group sufficiently distinct from the other agarics to merit its own Order, Boletales. I prefer to keep these mushroom-like organisms within the Agaricales (conveniently reducing the number of Orders you need to memorize). Boletes, as they are usually called, are often large, solid agarics, with the hymenium lining a layer of vertical fleshy tubes that (diagnostically) can be easily separated from the flesh of the cap. The often swollen stipe frequently has net-like or warty ornamentation (Fig. 5.7 D), and sometimes a partial veil. The spores are elongated, and yellowish-brown in mass. There are no clamp connections on the hyphae. Most boletes are ectomycorrhizal.

*Boletus edulis* is the famous edible ‘Steinpilz’ or ‘cep’ of Europe, and fortunately also occurs in North America. It is either a rather variable species, or more probably a
species complex. Many other boletes are also eaten, though species with orange or reddish pore-mouths, like those of *Boletus frostii*, *Boletus satanas*, and many other species, must be avoided. Those whose flesh turns blue when bruised should also be treated with caution. *Tylopilus felleus* is visually spectacular, but gastronomically a bust. It often occurs in large numbers under conifers, raising the expectations of the onlooker, but hopes are dashed when the pink tube mouths are seen, and we realize that we have found ‘the bitter bolete.’

The blue-staining *Gastroboletus* is alleged to be a sequestrate derivative of *Boletus*, though it is sometimes placed in the Xerocomaceae. *Suillus spraguei* demonstrates the partial veil that is found in many species of this genus, as does *Suillus grevillei*. Many species of *Suillus* also have viscid caps. *Truncocolleumella*, which has a vestigial stipe, and *Rhizopogon*, which does not, are sequestrate, hypogeous offshoots of *Suillus*. Like the parent genus, they are important ectomycorrhizal partners of conifers in western North America. *Rhizopogon parksii*, a very common western species, has a spongy, lacunose basidioma. The spores, however, are just like those of a *Suillus*, and DNA studies have established that *Rhizopogon* is very closely related to *Suillus*.

m) Family Gomphidiaceae. This mycorrhizal family has (1) viscid caps, (2) decurrent gills (not tubes), (3) a dark grey to brownish-black spore print and (4) microscopic structure that shows it is closely related to the Boletaceae. *Gomphidius* has white flesh; that of *Chroogomphus* is pink to orange. Sequestrate forms have arisen from both genera. This family is common in western North America, much less so in the east.

n) Family Gyrodontaceae. This family superficially resembles the Boletaceae, but (1) the tubes are shallow and not easily detached; (2) the spore print is yellowish or olivaceous brown; (3) the spores are subglobose to ellipsoid; and (4) the hyphae have clamp connections. *Fuscoboletinus*, *Boletinus*, *Gyrodon* and *Gyroporus* are representative genera.

o) Family Paxillaceae. Like the Gomphidiaceae, this mycorrhizal family (1) has gills, not tubes, but (2) the gills are easily separated from the flesh of the cap. (3) The gill trama is divergent and gelatinized. (4) The spore print is brown or white, and (5) the spores are ovoid to ellipsoid. The common species, *Paxillus involutus*, is a symbiont of conifers, and is easily recognized by its inrolled cap margin, its decurrent gills and the brown stains that appear after it has been handled. *Hygrophoropsis aurantiaca* is known as the ‘false chanterelle’. It has conspicuously forking gills.

p) Family Strobilomycetaceae. The cap of *Strobilomyces floccopus* is (1) greyish-black, (2) with large, shaggy scales, and (3) the tubes are grey, turning reddish when bruised. (4) The spore print is black, and (5) the spores are ornamented with a network of ridges. The genus *Boletellus* appears to have given rise to no fewer than four sequestrate forms: *Austrogauieteria*, *Chamonixia*, *Gautieria* and *Protogautieria*.

If you want to know more about the strange and fascinating sequestrate agarics – taxa derived from no fewer than fourteen families of agarics – which no longer shoot their spores, you can read two papers dealing with this issue: Kendrick, B. (1994) Evolution in action: from mushrooms to truffles. *McIlvainea* 11: 34-38 (part 1) and 39-47 (part 2).

In 1989 Canada joined the many countries that have issued stamps depicting macrofungi, producing handsome (if slightly stylized) stamps of *Clavulinopsis fusiformis*, *Boletus mirabilis*, *Cantharellus cinnabarinus* and *Morchella esculenta*. (I have been trying to get the Canadian post office to bring out some stamps on moulds, thus far without success, despite the important roles these fungi play as producers of penicillin, griseofulvin, cyclosporine, aflatoxin, etc.)
The foregoing is no more than a gesture sketch of the world of the agarics. If you want to learn more about what many people consider the most fascinating of all fungi, you must buy or borrow one of the field guides listed under ‘Further Reading’ at the end of this chapter. The large tome by René Pomerleau has all the minutiae a Northeasterner needs (though the colour illustrations are poor), but the pocket-sized Audubon Guide by Lincoff, though less detailed, covers the whole continent and can go anywhere with you. The larger-format *Mushrooms of North America* by Roger Phillips, published in 1991, has over 1,000 colour photographs, and includes many more species of, for example, *Cortinarius* (93), *Amanita* (41), *Lactarius* (64) and *Russula* (81), than other guides. *Mushrooms Demystified* by Arora, though oriented toward western North America, is a mine of useful and often amusing information for all mushroom-fanciers; it also covers a wide range of taxa (even dealing with many sequestrate forms). *The New Savory Wild Mushroom* has excellent colour photographs, but is mainly useful to those in the Pacific Northwest. The latest addition to these field guides is *Fungi of Eastern Canada and the northeastern United States* by George Barron. It covers over 600 species of fungi and is illustrated with more than 650 photographs.

In addition to agarics, these books cover the more conspicuous Gasteromycetes, Ascomycetes and Aphyllophorales. Some of the larger and more difficult genera call for separate keys, and those to the northeastern species of *Russula* by Kibby and Fatto are excellent examples. “Matchmaker” is a new, profusely illustrated synoptic key to 2,000 mushrooms on CD-ROM (see Bibliography at the end of this chapter).

**Series Gasteromycetes**

Although many kinds of sequestrate fungi can be traced to their agaricoid origin, many others probably evolved so long ago that it is no longer possible to trace their ancestry with any degree of certainty. For these, which we call Gasteromycetes, we have erected special Orders, based on the mode of passive spore dispersal into which they have evolved. I think you will agree that if these groups have any agaric ancestry, it is well concealed. All have non-shooting holobasidia.

*Limnoperdon*, a minute floating gasteromycete, occurs in woodland ponds. Its basidia are produced inside a tiny, entirely closed, hollow basidioma, so there would be no point in the spores being forcibly shot from the basidium. The non-shooting nature of the basidium is apparent from the symmetrical way in which the spores are mounted on the sterigmata (remember that typical shooting basidia have their spores asymmetrically mounted as an integral part of the shooting mechanism). Fig. 5.8 A-E shows non-shooting basidia of a range of gasteromycetes.

(5) **Order Sclerodermatales**: 11 genera, 38 species. The ‘earthballs’ (as opposed to ‘puffballs’). Here the spore mass (*gleba*) has small spore-containing cavities (*locules*) with no real hymenium, and is powdery at maturity, with no true stipe or capillitial threads. In the common genus *Scleroderma* the spore mass is blackish at maturity, and the basidioma has no ostiole.

The separate locules are clearly visible in *Pisolithus tinctorius* (Fig. 5.8 F), which is perhaps the most famous of all ectomycorrhizal fungi, since it helps conifers and eucalypts to thrive on particularly unfavourable sites. It has been the subject of many research projects, as you will read in chapter 17. I have found this fungus fruiting at various places in North America, Australia and South Africa. The basidiomata are often lumpy and almost shapeless, and it is sometimes called the ugliest fungus in the world, despite its excellent qualities as a mycorrhizal symbiont. Mature fruit bodies have been collected as a source of spore inoculum and, as I have seen, can also be used in a hot-weather version of a snowball fight.
Sphaerobolus stellatus, of the atypical family Sphaerobolaceae, has a six-layered peridium. At maturity, the innermost layer and part of the third layer liquefy, and the second layer takes up the free water, eventually evertting suddenly and throwing the gleba up to six metres toward the light. These are the only gasteromycetes in which a form of active spore dispersal has been re-evolved. But notice that evolution did not reverse itself – the odds against that ever happening are astronomical, and I know of no documented cases.

(6) Order Melanogastrales: 9 genera, 46 species. A completely hypogeous group, in which the gleba has many locules with no true hymenium, and whose contents are mucilaginous at maturity. Locules are separated by distinct white septa. Basidiospores are symmetrical and have a fairly broad attachment scar, both signs that they are not actively shot away from the basidia. Melanogaster and Leucogaster are representative genera.

Fig. 5.8 Holobasidiomycetes which lack active spore discharge. A: Agaricales; B,H,I: Lycoperdales; C,F: Sclerodermatales; D,G: Tulostomatales; E: Phallales.
(7) **Order Tulostomatales**: 9 genera and 75 species of stalked puffballs, with dry, powdery gleba. *Tulostoma* looks a bit like a rabbit pellet on a stalk, but has a built-in ostiole (Fig. 5.8 G). *Calostoma* has a gelatinous stipe and a most peculiar stellate ostiole rimmed with red pigment — the only puffball that wears lipstick. I first saw this fungus in New Zealand, but have found similar species in the Carolinas.

(8) **Order Lycoperdales**: 26 genera, 260 species. These are the common and well-known puffballs and earthstars, with powdery glebas. Though most are saprobic in soil and on rotten wood, some may be ectomycorrhizal. In contrast to the Sclerodermatales, the glebal cavities are lined by a hymenium when young. The mature spore mass is usually khaki-coloured and mixed with capillitial filaments. The peridium has two or more layers, and usually develops an apical ostiole. The papery inner peridium can be compressed by raindrops, expelling air and spores through the ostiole. *Lycoperdon* (Fig. 5.8 H) is the best-known genus, to which most common puffballs belong. *Langermannia* (formerly *Calvatia*) *gigantea* is the giant puffball. Before the spore mass (gleba) matures, and while the interior looks like white marshmallow, this fungus is often collected and eaten. A Canadian specimen collected in 1987 held the world record until 2000 for the largest edible fungus — 2.64 metres in circumference and weighing 22 kg.

*Geastrum* species (Fig. 5.8 I) are known as earthstars. In this genus the thick outer peridium splits stellately as it dries out, and the segments fold back in order to raise the gleba, in its inner, papery peridium, above the dead leaves that might otherwise prevent the puffball mechanism from working.

(9) **Order Nidulariales**: 5 genera, 60 species. These are the bird’s nest fungi, in which the basidioma has been modified to become a splash-cup spore dispersal mechanism. The basidiospore mass, or gleba, is divided up among several individual ‘eggs’ (more formally, peridioles). The kinetic energy of raindrops is focused and reflected by the funnel-shaped basidioma, and the rebounding water carries the peridioles with it. *Crucibulum, Cyathus, Nidula* and *Nidularia* are representative genera.

In *Cyathus* (Fig. 5.9 A) the peridioles are attached to the wall of the basidioma by a long thread, most of which is folded up inside the stipe of the peridiole. When the peridiole is splashed out, the thread unwinds rapidly, trailing behind. At the end of the thread is a sticky blob which acts to anchor the peridiole to whatever it strikes.

(10) **Order Phallales**: 25 genera, 45 species. These are the stinkhorns, whose spores are dispersed by animal vectors. The gleba is slimy and really does smell bad, so it attracts flies which wallow in the mess, eating some spores and carrying others away on their feet. Although two well-known stinkhorns, representing the genera *Phallus* and *Mutinus*, are fairly common in North America, the most bizarre genera are commoner in Australasia and the tropics. All stinkhorns develop in a gelatinous matrix within a membranous ‘egg-shell’ or peridium, but when they ‘hatch,’ their mature fruit bodies can be strikingly different.

*Phallus* (Fig. 5.9 D) and *Mutinus* (Fig. 5.9 B) have the simplest morphology: the stipe elongates rapidly, carrying their respectively thimble-shaped and conical heads (often called receptacles), into the air, where they can release their effluvium and attract the flies more easily. Europeans have sufficient knowledge of these fungi to enjoy cartoons of them. North Americans, to whom they are less familiar, look at such artwork askance.

The genus *Dictyophora* (whose name means ‘net-bearer’) does indeed have a visually striking lacy skirt hanging below the receptacle. My guess is that this is a landing platform for flies queuing up for a sample of gleba. In *Anthurus* (Fig. 5.9 C), the gleba is at first central in the egg. Later the spore mass covers the inner side of several octopus-like
arms. In *Clathrus* (Fig. 5.9 F) the arms remain fused, and in some species form an open lattice, again with the gleba on the inside. *Aseroe* (Fig. 5.9 E) is surely one of the most flamboyant members of a truly spectacular Order. Bright orange-red extensions of its receptacle radiate out like the petals of a flower, and also look rather like meat, providing a diverse range of visual as well as olfactory clues to would-be vectors, which can be drawn from among the meat-eaters (e.g. wasps), the nectar-eaters (e.g. butterflies) and the visitors to excreta. *Hysterangium* is hypogeous, so the gelatinous layer found in most Phallales is not well-developed, and there is no dramatic rupture of the peridium at maturity. But the affinities of this reclusive sequestrate genus with the otherwise exhibitionistic Phallales are accepted.

![Fig. 5.9 Gasteromycetes. A: Nidulariales; B-F: Phallales.](image-url)
Classes Phragmobasidiomycetes and Teliomycetes

The two remaining classes in the subphylum Basidiomycotina are very different. One is of no (or very little) economic importance, the other causes many serious crop diseases. Both have basidia that are divided into four compartments by septa, each compartment giving rise to a single basidiospore. In Class Phragmobasidiomycetes, the basidia are borne on some kind of basidioma, but in Class Teliomycetes, they arise from overwintering spores. Members of these two Classes often have the ability (1) to form secondary spores from their primary spores; (2) and/or to produce yeast-like cells. Most Holobasidiomycetes can do neither of these things (but see p. 114).

Class Phragmobasidiomycetes

This group contains four Orders: Tremellales, Auriculariales, Septobasidiales and Tulasnellales, which all have basidia subdivided by septa.

1) Order Tremellales: These are jelly fungi generally found on dead wood. Long considered harmless saprobes, they have recently been unmasked as vicious mycoparasites of other wood-inhabiting fungi. The basidia (Fig. 5.10 A) are often described as ‘cruciately septate,’ being vertically divided into four compartments. Each of these develops a long outgrowth that extends to the surface of the gelatinous matrix and produces a ballistospore. The most recent interpretation of these ‘basidia’ is that the vertical septation separates the nuclei into four cells that can be called basidiospores, and that the long ‘epibasidia’ which grow up to the surface of the jelly are actually germ tubes. This would mean that the ‘basidiospores’ are actually secondary spores, results of a form of ‘germination by repetition,’ a phenomenon so common in the phragmobasidiomycetes that it is often used as a diagnostic character.

The basidiomata of *Tremella* are often irregularly shaped (Fig. 5.10 A). Other representative genera are *Phlogiotis*, the rather attractive scoop-shaped ‘apricot jelly,’ and *Tremellodon*. But in *Pseudohydnum*, convergent evolution has produced a form reminiscent of certain holobasidiomycetes. *Pseudohydnum* has its hymenium on downward-pointing teeth like those of the Hydnaceae (Aphyllophorales), but the rubbery texture of its basidioma, and the cruciately septate basidium, give the game away – it is undoubtedly a member of the Tremellales.

2) Order Auriculariales: 5 genera, 16 species. Members of this Order are easily identified by their gelatinous, ear-like basidiomata arising from wood (Fig. 5.10 B). The elongated basidia are divided by transverse septa, and each of the four compartments develops a slender tubular outgrowth that produces a basidiospore when it reaches the surface of the gelatinous matrix. The Chinese call members of the genus *Auricularia* ‘cloud ears’ or ‘tree ears,’ and use them in cooking, largely for their interesting texture. We have recently discovered that they contain a substance which reduces the clotting propensities of blood, and so may offer some protection against heart attacks.

3) Order Septobasidiales: 2 genera, 175 species, mostly in *Septobasidium* (Fig. 5.11 A). This Order also has transversely septate basidia, but its basidiomata are not gelatinous, and it parasitizes scale insects. These do not die, but become sterile. They are buried in a weft of fungal hyphae that produces basidia on its surface and provides shelter for other healthy scales.

4) Order Tulasnellales: This small Order is interesting to us mostly because it has yet another variation on the phragmobasidium. In *Tulasnella* the four developing sterigmata swell up and each becomes separated from the body of the basidium by a secondary septum (Fig. 5.11 B)
Class Teliomycetes

This group comprises two distantly related Orders, Uredinales and Ustilaginales, which produce no basidiomata and have simple septal pores with pulleywheel occlusions (Fig. 5.1 D) rather than the dolipores characteristic of most other basidiomycetes.

(1) Order Uredinales: 164 genera, 7,000 species (3,000 in one genus – Puccinia). The rust fungi are all obligately biotrophic on vascular plants and often have very narrow host ranges, being restricted to a single family, a single genus, or even a single species. Although they have obviously co-evolved with their hosts for millions of years and don’t usually kill them, rust fungi can severely reduce yields of our domesticated plants, particularly the cereals on which we are so dependent. The rust fungi produce basidia from overwintering spores (teliospores), so they don’t form basidiomata. But they do produce no fewer than five different kinds of spore, each specialized for a particular step or phase in the life cycle. And they often alternate between two hosts, which tend to be from taxonomically distant groups. This is important information, because as you will see in chapter 12, our efforts to control many diseases of our food crops depend on our knowl-
edge of the life history of the pathogens. In any case, these most complex of all fungal cycles are intrinsically fascinating.

*Puccinia graminis* subspecies *tritici*, the fungus causing black stem rust of wheat, can exemplify *macrocyclic*, *heteroecious* rusts (those producing all five spore forms and moving back and forward between two different hosts). The different stages of the life cycle are shown in Fig. 5.12. Basidiospores, which are of + and - mating types, land on a young leaf of barberry (*Berberis*) in spring, and initiate localized monokaryotic infections. The hyphae are intercellular, but they send haustoria into host cells to absorb food. Soon, these monokaryotic mycelia develop tiny flask-shaped *spermagonia* (stage 0) in the upper layers of the leaf. They produce only small brown spots and don’t do any significant damage to the barberry. Each spermagonium forms innumerable tiny *spermia* which ooze out in a sweet-smelling nectar. A tuft of *receptive hyphae* also grows out from the neck of each spermagonium. Insects are attracted by the nectar, and walk or fly from one spermagonium to another, unwittingly transferring spermia of each mating type to receptive hyphae of the other type. This process, which is somewhat analogous to pollination, initiates the *dikaryophase*. The dikaryotization spreads to the lower surface

![Diagram of fungal life cycles](image-url)
of the barberry leaf, where the fungus has already produced the primordia of cup-like structures called aecia (stage I) – two are shown in this section.

The flower-like aecia burst through the host epidermis, and liberate dikaryotic aeciospores – but these spores can’t infect the barberry. Only if they land on a wheat plant (*Triticum*) can they establish new dikaryotic infections. That is why I call them ‘transfer spores.’ The dikaryotic mycelia in the wheat plant soon produce uredinia – pustules of reddish-brown, dikaryotic urediniospores (summer spores – stage II) – which again burst through the host epidermis and are wind-dispersed to other wheat plants.

Note that the urediniospores are unicellular and rather thick-walled, but have distinct equatorial germ pores. The many new infections generated by these spores soon produce further inoculum, and waves of urediniospores, borne on the prevailing winds, cause the massive epidemics of wheat rust that periodically sweep North America.

Toward the end of summer, these same pustules switch over to producing another kind of spore, the dark, two-celled, thick-walled teliospores (winter spores – stage III). Each cell of the teliospore is binucleate at first, but karyogamy soon occurs and the spores overwinter in the genuinely diploid or zygotic condition. In spring, each cell germinates and gives rise to a short hypha which becomes a transversely septate basidium (Fig. 5.11 C) (rather like those of the Auriculariales and Septobasidiales). Each cell develops a short sterigma which in turn bears a basidiospore (stage IV). These are borne asym-
metrically, and are shot away in typical basidiomycete manner. They must land on a barberry leaf if the cycle is to continue.

Some rust fungi don’t produce all five spore forms, and are described as microcyclic. Some complete their cycle on a single host, and are called autecious. *Puccinia poae-nemoralis*, a normally heteroecious rust fungus, persists in the Canadian arctic through the ability of its urediniospores to overwinter. It never forms teliospores, and so needs no alternate host. Some tropical rust fungi don’t form teliospores either, but in this case it is because there is no need for an overwintering spore.

Stage I (aecia) and stage II (uredinia) may be regarded as the two asexually reproductive stages (anamorphs) of a rust fungus. Stage III, the teliospore, is regarded as the sexual state or teleomorph, so the host on which these spores develop is called the primary host. In the case of *Puccinia graminis* subspecies *tritici*, wheat (*Triticum*, Poaceae, Monocots) is the primary host, and barberry (*Berberis*, Berberidaceae, Dicots) the alternate host.

Because of the threat they pose to our food supplies, the cereal rusts have been intensively studied, and they have repaid that scrutiny with a rich harvest of taxonomic and genetic information. The species *Puccinia graminis* attacks many different grasses. Several subspecies have been recognized by their apparent restriction to individual grass genera, e.g. *P. graminis* ssp. *avenae* on oats (*Avena*), *P. graminis* ssp. *hordei* on barley (*Hordeum*), and, of course, *P. graminis* ssp. *tritici* on wheat (*Triticum*). Each of these subspecies is subdivided into many physiological races which differ in their ability to attack specified commercial varieties of the host genus. *Puccinia graminis* ssp. *tritici* has over 200 such races, and new ones are discovered every year. Wheat breeders have to work hard to stay one jump ahead of the pathogen. Breeding of resistant plants is discussed in chapter 12.

Some heteroecious rusts move between angiosperm and gymnosperm hosts, and sometimes it is the alternate host, rather than the primary host, that is economically important. *Gymnosporangium* is an interesting heteroecious rust. One of its hosts is a rosaceous plant like pear. It produces spermagonia on the upper side of the leaves. These liberate both nectar, to attract arthropods, and spermatia (non-motile, but effectively male gametes) which the visiting animals transfer to spermagonia of the opposite mating type, whereupon dikaryotization happens. After dikaryotization, the fungus goes on to produce its aecia on the same lesion, but on the other side of the leaf. On another rosaceous host, serviceberry (*Amelanchier*), it produces aecia on the hypertrophied fruit. The aeciospores can infect only the other host, a conifer such as juniper (*Juniperus*), on which the spectacular gelatinous telial horns are produced (these are obvious only during wet weather).

A similar alternation happens in the genus *Cronartium*. *Cronartium ribicola* (blister rust of white pine) produces its spermatia and aeciospores on five-needled white pines (eastern white pine, *Pinus strobus*, and western white pine, *Pinus monticola*), and its urediniospores and teliospores on wild currant (*Ribes*). The aecial hosts of *Cronartium comandrae* (Comandra blister rust), are two- and three-needled pines, including *Pinus ponderosa* (ponderosa pine), and *Pinus contorta* var. *latifolia* (lodgepole pine). The telial hosts are the herbs California comandra (*Comandra umbellata* var. *californica*) and Bastard toadflax (*Comandra livida*). The name of these diseases, ‘blister rust,’ refers to the conspicuous aecia, and it is the perennial aecial cankers on the pines that gradually spread and often eventually girdle and kill the tree. *Cronartium fusiforme*, another blister rust, alternates between various southern pines (on which it develops its aecia) and oaks (*Quercus* spp). *Chrysomyxa arctostaphyli* moves between black spruce (*Picea mariana*),
on which it produces its aecia, and *Arctostaphylos*, an ericaceous shrub on which it produces its telia.

The genus *Phragmidium* commonly occurs on members of the Rosaceae. I found a telial specimen in the garden, on one of my wife’s precious roses. She was not impressed. However, I was nostalgic about it, because the first microscopic fungus I ever collected, way back in the 1950s, was a *Phragmidium* producing clusters of its dark, stalked, phragmosporous teliospores on blackberry leaves. When I mounted the spores I immediately assumed it was a dark-spored hyphomycete (see chapter 4a). I can’t remember who disabused me of this notion, but if you get the Class and Order right, this is one of the easiest rusts to identify. The teliospores from our rose leaf had a distinct, though colourless, stalk, six darkly pigmented cells, and an apical spine. These characters and its host preference identified it as *Phragmidium mucronatum*, which is the commonest of the nine species that occur on roses. These teliospores are big, as fungal spores go: the body of the spore is about 77 microns long.

Some rusts fungi are systemic, spreading throughout their host plants before sporulating. This means that the sudden eruption of uredinia all over the leaves can be rather spectacular. In Java I found coffee leaves infected with the infamous coffee rust, *Hemilaee vastatrix*, which causes defoliation of the coffee plants. It was the invasion of this rust fungus that caused Sri Lanka (formerly called Ceylon) to abandon coffee as its prime crop, and make the radical shift to growing – and exporting – tea.

(2) **Order Ustilaginales**: 60 genera, 1,000 species (300 in *Ustilago*). Like the rust fungi, the smut fungi are all parasites of vascular plants, and produce basidiospores on transversely septate basidia arising from overwintering teliospores. But the two groups differ in many respects, as Table 5.1 shows.

a) Family Ustilaginaceae. In this group the teliospore is karyologically equivalent to that of a rust fungus, so the short hypha arising from a germinating teliospore of *Ustilago* becomes 3-septate, and buds off a yeast-like basidiospore from each compartment (Fig. 5.11 D). Compatible elements soon fuse to restore the dikaryon. In homothallic species this can rather conveniently involve basidiospores from the same basidium, or a basidiospore can fuse with a cell of the basidium, or two cells of the same basidium may fuse, or teliospores may germinate and form a mycelium between whose hyphae fusions can occur. Many smut fungi, however, are heterothallic, so fusions must be between cells of different and compatible parents.

The teliospores of *Ustilago violacea* are present on the seeds of its host, *Silene* (Caryophyllaceae), and germinate when the seeds do. After the dikaryotization process described above, the newly dikaryotic mycelium infects the seedling. Although the mycelium becomes systemic, spreading throughout the host, it incites no pathological symptoms until the flowers develop. Then the pollen is replaced by a mass of dikaryotic mycelium, which eventually disarticulates into teliospores. The disease is called anther smut.

Many other smuts are also organ-specific: in corn smut, caused by *Ustilago maydis*, some or all kernels are replaced by grossly swollen masses of black teliospores. In onion smut, caused by *Urocystis cepulae*, the teliospores develop in the bulb. Note that the organ attacked (and often replaced) by smut fungi is always one into which the plant directs high-energy resources – anthers, seeds, bulbs. Since humans are often interested in the host storage organs as sources of food, it may not be too surprising that frustration at the apparent loss of that food led people to sample the fungus instead. As you can read in chapter 18, at least two smuts are widely eaten: the black spore masses of corn smut (*Ustilago maydis*) are regarded as a delicacy in Mexico, and *Ustilago esculenta*, which causes hypertrophy in the stems of wild rice, is widely eaten in China.
Table 5.1 Differences between Rust and Smut Fungi

<table>
<thead>
<tr>
<th>Uredinales</th>
<th>Ustilaginales</th>
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</thead>
<tbody>
<tr>
<td>1) Teliospores terminal</td>
<td>Teliospores intercalary</td>
</tr>
<tr>
<td>2) Basidiospores 4, shot from sterigmata</td>
<td>Basidiospore number variable, not on sterigmata, not discharged</td>
</tr>
<tr>
<td>3) Spermagonia produced (sex organs)</td>
<td>No sex organs, any two compatible cells can fuse</td>
</tr>
<tr>
<td>4) Clamp connections absent</td>
<td>Clamp connections common</td>
</tr>
<tr>
<td>5) Often require 2 hosts</td>
<td>Never require 2 hosts</td>
</tr>
<tr>
<td>6) Obligately biotrophic</td>
<td>Facultatively biotrophic, yeast-like in culture</td>
</tr>
<tr>
<td>7) Infections usually localized</td>
<td>Infections usually systemic</td>
</tr>
<tr>
<td>8) Teliospores in telial sori, location unspecific</td>
<td>Teliospores replace host organ, e.g., ovary, anther</td>
</tr>
<tr>
<td>9) Attack ferns, gymnosperms and angiosperms.</td>
<td>Attack only angiosperms</td>
</tr>
</tbody>
</table>

b) Family Tilletiaceae. Here, events are physically more compressed: karyogamy, meiosis and mitosis all happen inside the teliospore. When this germinates, the resulting basidium produces a cluster of slender, parallel basidiospores from its apex (Fig. 5.11 E). These soon copulate in pairs to restore the dikaryon. *Tilletia caries*, the cause of 'bunt' or stinking smut of wheat, is just as important an economic problem as stem rust, because it has so far proved impossible to breed strains of wheat resistant to this fungus.

Now I'll wrap this long chapter up with a key to the more common Orders of basidiomycetes. If you'll read through it, it will help you to recap the major characteristics I have shown you in the text and pictures above.

**KEY TO SOME COMMON ORDERS OF BASIDIOMYCETES**

1. No basidioma; basidia solitary (free), or on individual hyphae...............................(see yeasts)
2. No basidioma; basidia arising from resting spores (class Teliomycetes)....................2
3. No basidioma; basidia in a layer on surface of host plant.......................................Exobasidiales
4. Basidioma produced..............................................3
2 ‘Smut’ fungi; autoecious, basidiospores not discharged, clamps common, resting spores intercalary; grow in culture. \textit{Ustilaginales}

2 ‘Rust’ fungi; often heteroecious, basidiospores discharged, clamps absent, resting spores terminal, obligately biotrophic. \textit{Uredinales}

3 Basidia vertically or transversely septate (class Phragmobasidiomycetes) \textbf{4}

3 Basidia not divided by septa (class Holobasidiomycetes) \textbf{5}

4 Basidia divided vertically into 4; each with a long apical extension, bearing one spore (jelly fungi). \textit{Tremellales}

4 Basidia divided transversely into 4; each cell with a lateral outgrowth bearing one spore (ear fungi). \textit{Auriculariales}

5 Basidiospores obliquely attached to sterigmata; hymenium exposed at maturity and spores forcibly discharged (give spore print) (series Hymenomycetidae) \textbf{6}

5 Basidiospores symmetrically attached to sterigmata, or sterigmata absent, spores not discharged (no spore print) (sequestrate Agaricales and series Gasteromycetae) \textbf{8}

6 Basidia slender, with two long extensions (tuning fork basidia) (jelly fungi) \textit{Dacrymycetales}

6 Basidia usually with 4 short sterigmata, no long extensions \textbf{7}

7 Hymenium covering vertically oriented, radially arranged lamellae or lining vertically oriented fleshy tubes (agarics and boletes). \textit{Agaricales}

7 Hymenium in other configurations \textit{Aphyllophorales}

8 Basidioma agaricoid, but not releasing spores; or micro-anatomical features establishing relationships to agarics or boletes \textit{sequestrate Agaricales}

8 No clear derivation from Agaricales or other groups (series Gasteromycetae) \textbf{9}

9 Basidiospore mass (gleba) slimy, stinking, exposed on receptacle (stinkhorns, etc) \textit{Phallales}

9 Gleba not slimy and evil-smelling \textbf{10}

10 Gleba enclosed in several small, separate peridioles; basidiomata tough and deeply funnel-shaped or cup-shaped (bird’s nest fungi) \textit{Nidulariales}

10 Not as above \textbf{11}
11 Spore mass powdery, drab or khaki
coloured, peridium 2-layered, inner
peridium papery, usually with ostiole
(puffballs) .................................................. 12

11 Spore mass dark, peridium 1-layered,
 thick, no ostiole (earth-balls) ...................... Sclerodermatales

12 Basidiomata more or less sessile
 or stalk not distinct .................................. Lycoperdales

12 Basidiomata prominently stalked ............ Tulostomatales

Further Reading on Basidiomycetes

Realm of Yeast-like Fungi. (Eds.) G.S. de Hoog, M.Th. Smith and A.C.M.
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Coker, W.C. and Couch, J.N. (1928) Gasteromycetes of the Eastern United States and
Memoirs 1.
London.
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Hill.
American Phytopathological Society, Minneapolis.
Vols. 1-6. Fungiflora, Oslo.
Lochside Drive, Sidney, BC, Canada V8L 1M8
Whole Fungus, Vol. 2. Nat. Mus. Canada, Ottawa (now available only from
Mycologue, 8727 Lochside Dr., Sidney, BC, Canada V8L 1M8.)


The “Matchmaker” visual basic program by Ian and Eli Gibson contains descriptions of over 2,000 species of gilled mushrooms, 680 of them linked to 1,269 colour photographs. A series of menu screens permit entry of characters and subsequent searches for matches. The program thus offers a synoptic key for mushroom identification. There are also 773 colour photographs of 399 non-gilled taxa. This program is available on CD-ROM with *The Fifth Kingdom*, from Mycologue Publications (see www.mycolog.com).