

Red-brown blushing morel—*Morchella rufobrunnea* (fig. 5).

Description—**Head:** conical to subconical to ovoid when mature. **Ribs:** whitish to grayish when young, becoming yellowish, brownish, or brownish-yellow with age. **Pits:** vertically elongate when young, becoming irregularly shaped with age. **Stalk:** irregularly wrinkled near base with minute dark granules toward the top; whitish to cream, pale gray, darker grayish brown, yellowish toward base, blushing in irregular spots brown, brownish orange, or pinkish red to ferruginous when injured or maturing (both head and stalk), sometimes almost completely reddish brown. **Spore size:** (19-) 20–24 (-25.5) x (13-) 14–16 (-17) μm .

Ecology—Growing in moist subtropical oak, sweetgum, white-alder (*Clethra*), and alder forests in the Xalapa region of Mexico. Perhaps also along coastal California in landscaping mulch.

Comments—Kuo (2005, 2006) suggested that what has been identified as *M. deliciosa* in California is actually *M. rufobrunnea*. He also suggested that *M. rufobrunnea* was the morel that Ower described cultivating in his first patent (Ower and others 1986), rather than *M. esculenta*. At the time of the patent, *M. rufobrunnea* had not yet been described and was not yet suspected as a separate species along coastal California. *M. guatemalensis* and *M. herediana* are other morel species that occur in subtropical regions of Mexico and Central America, but do not range further into North America (Guzmán and Tapia 1998).



Figure 5—
Red-brown
blushing
morel.

Half-free morel—*Morchella semilibera* (fig. 6).

Description— **Head:** often taller than broad, subcylindric to broadly conic with a rounded to truncated apex when young; often broader than tall in age; up to one-half of the lower part of the head and margin free of the stalk and forming a skirt, otherwise attached to stalk in the same manner as other morels. **Ribs:** often running from the top to the bottom of the head with irregular cross-ribs; ribs broad, flat, moist to velvety in youth, and collapsing and darkening to dark grayish brown or black in age. **Pits:** grayish tan when young, grayish tan to tan at maturity. **Stalk:** ivory white to dull creamy yellow, surface scurfy as if dusted with fine cornmeal or bran, elongating to 2.5 to 3 times the length of the head with age; tapering toward the apex, swelling especially at the base, and becoming fragile. **Spore size:** (19.5-) 22.5–26 (-30) x (12-) 14–17 (-21) μm .

Ecology—Occurring under conifers, cottonwoods, and alder. Fruiting is erratic.

Comments—The half-free morel in the western North America might be a different species than that in the east. Kuo (2005) mentioned a half-free morel from Oregon that differs genetically from the eastern half-free morel. He also suggested that both are different from the European *M. semilibera*. If so, new scientific names might be forthcoming, but the half-free morel is morphologically distinctive and for now we chose to retain the use of the scientific name *M. semilibera*. The habitat of this morel is similar to both the edible yellow morel and the potentially poisonous *Verpa bohemica* or “early morel.” Be sure to check whether the head is attached to the stem part way down. This is best discerned by cutting the specimen in half lengthwise from top to bottom for a longitudinal-section view. If the head is attached to the stem halfway down, it is an edible half-free morel; if the head is attached only at the top of the stem, it is a potentially poisonous *Verpa*.



Pamela Kaminski, <http://www.pamelasmushrooms.com/>

Figure 6—Half-free morel (*Morchella semilibera*).

Potentially harmful look-alikes—Two closely related genera of mushrooms have potentially harmful species that could be mistaken for morels by the inexperienced harvester. These are *Verpa* (the thimble morels) and *Gyromitra* (the false morels or lorichels). Some people consume some species in these genera, and *Verpa bohemica* is sometimes sold commercially. However, some species in these genera are potentially toxic, especially if improperly cooked, and are best avoided. Arora (1986), Kuo (2005), and Weber (1988) provide good descriptions of these genera and species, as do most mushroom field guides. Figure 7 illustrates key differences in appearance between *Morchella* species and representative *Verpa* and *Gyromitra* species. Species in the related genera *Helvella* (elfin saddles), *Disciotis* (veined brown cup fungus), and *Discina* (pig’s ears) are not shown because their features are easily distinguished from the pitted and ridged heads of morels. Readers are encouraged to familiarize themselves with the differences among all these genera before collecting true morels. This publication is not an identification guide. The reader is responsible for her or his own health. For further information about the risk of eating these mushrooms, see the section on “Toxins and Contaminants.”

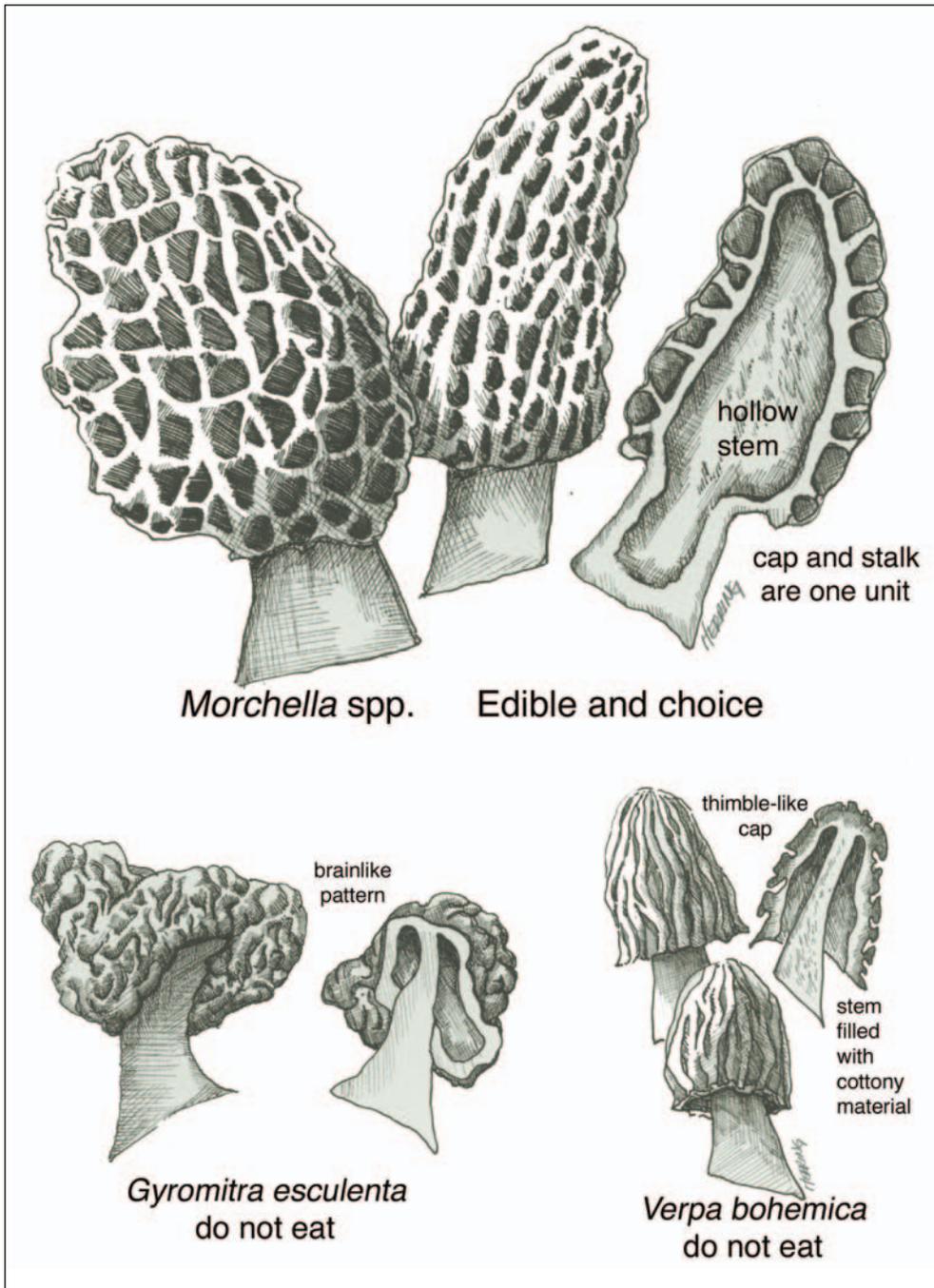


Figure 7—Comparison of three genera sometimes referred to as “morels”: *Morchella*, *Gyromitra*, and *Verpa*. Some species in the genera *Gyromitra* and *Verpa* contain poisonous compounds and should be avoided. Illustrations by Margaret Herring. Reprinted from Wurtz and others (2005: 8).

To understand how morels seem unique among edible forest fungi in their adaptations, it is necessary to understand their life cycle, modes of nutrition, and reproductive strategies.

Biology

Overview—The broad ecological amplitude and environmental plasticity discussed by Wedin and others (2004) were considered adaptations to environments that experience unpredictable periods of rapid change. These strategies could prove useful to morels because they live in forests that experience episodic and catastrophic events such as wildfires, insect infestations, windstorms, volcanism, earthquakes, floods and, more recently, human-caused disturbances such as logging. To understand how morels seem unique among edible forest fungi in their adaptations, it is necessary to understand their life cycle, modes of nutrition, and reproductive strategies.¹⁴ We begin with a brief overview of how fungi live and reproduce in order to clarify how morels differ from most other harvested forest mushrooms. Then we describe the sequential stages of a morel life cycle.

Mushrooms are the reproductive structure of some types of fungi. They generally are fleshy and have a stem and a cap or (in the case of morels) a head. Mushrooms are one type of “sporocarp” meaning “spore-bearing fruit or structure.” Conks and truffles are examples of others. Sporocarps are also commonly called “fruit bodies” or “fruiting bodies” (American usage), although they are not technically “fruits” like those formed by plants.

Fungi are an entire branch on the tree of life, and actually shared a common ancestor with animals more recently than either did with plants. Many types of fungi, for instance yeasts, live as single cells. Others, such as the fungi that produce mushrooms, form filamentous multicellular structures that can be quite large. They do this by producing one-cell-wide strings of cells called hyphae (hypha singular). These threadlike hyphae often form dense interconnecting webs. Such webs of hyphae are called mycelia or mycelial colonies. A mycelium (singular) would typically represent a colony formed by a genetically distinct individual, and a collection of separate genetically distinct mycelial colonies would be called mycelia (plural). As we will see, morel mycelial colonies cannot simply be considered genetically distinct individuals as are the mycelia of many other mushroom-producing fungi.

¹⁴Technical mycological and genetic terminology is necessary to clearly explain these topics. Potentially unfamiliar concepts are explained and the glossary contains definitions for some of the less common terms we use. Ulloa and Hanlin (2000) and Kirk and others (2001) also provided definitions of mycological terms. King and Stansfield (2002) and Rédei (2003) can be consulted for genetic terminology, although a good, recent, standard dictionary is likely adequate. For the sake of brevity, many topics are incompletely explained, some scientific terminology is avoided, and exceptions to generalizations are sometimes not mentioned. Our intent is to provide a wide range of readers with a basic understanding of how morels differ from other important wild edible mushrooms; the implications that these differences have for understanding morel biology, ecology, and reproduction; and how the differences relate to managing forests for sustainable morel harvesting opportunities.

The mycelia of multicellular fungi live and grow inside their food sources. Because fungi do not have chlorophyll, they cannot produce their own food and must obtain it elsewhere. Fungi absorb nutrients directly through their cell walls from the nutritional substrate in which they grow. They also can excrete enzymes that break down resistant compounds (such as lignin in wood) into simpler molecules that can then be absorbed. Among fungi as a group, almost any other organism can serve as a source of food, even other fungi. Each species of fungus, however, usually concentrates on just a few types or sources of nutrition. These can be living or dead organisms. Fungi that eat (decompose) dead organisms are called saprobes. Fungi that kill or harm the live organisms they are consuming are called parasites. But many fungi have evolved mutually beneficial (symbiotic) relations with photosynthetic organisms such as plants, algae, and cyanobacteria. In these cases, the host organism derives some benefit from the fungus in return for providing the fungus with food. Perhaps the most important such symbiosis is mycorrhizal. The term mycorrhiza (mycorrhizae or mycorrhizas plural) literally means “fungus-root.” Mycorrhizae are dual organs of absorption common to almost all land plants. The fungal hyphae actually grow among, and in some cases into, the outer cells of the plant’s root tips. This is the zone where nutrients are exchanged between the fungus and the plant. The hyphae of mycorrhizal fungi also grow out into the soil, where their mycelial web creates what is functionally a vastly larger fine root system for the plant than it could produce itself. The fungus absorbs water and mineral nutrients with its mycelial network and shares them with the host plant, and in return the fungus absorbs carbohydrates from the plant’s roots. This symbiotic relationship between fungi and plant roots likely played a key role in the successful colonization of land by formerly aquatic plants. For years, morels were considered saprobes, decomposing organic matter in the soil, but as we will see, some are now believed to have the ability to form mycorrhizae and other unique fungus-root structures.

Fungi that produce mushrooms can reproduce both sexually and asexually (without sex). In effect, when most fungal cells divide, they are cloning themselves (producing a genetically identical copy). For instance, a hyphal cell from a mycelial colony might get stuck to the leg of an insect and deposited elsewhere. If that cell continues to divide, it would produce another genetically identical mycelial colony in the new location. Multicellular fungi primarily reproduce with spores; these are the fungal equivalent of seeds, although spores are single-celled and much smaller than seeds. Spores can be either sexual or asexual. Morels produce a type of asexual spore called a conidium (conidia plural, also called a conidiospore). These are the equivalent of a hyphal segment creating a new clonal colony, but the fungus does it intentionally by producing a spore, designed for dispersal, on a special hyphal

structure called a conidiophore. Asexual spores typically have the entire genetic complement of the mycelium that produces them. Whether asexual spores produced by morels have the entire genetic complement of the mycelium is not yet known.

One difference between sexual and asexual spores is that sexual spores typically have half the genetic material (haploid) of the mycelial colony that produced the sporocarp. Such haploid spores are produced by a process called meiosis, the same process that produces sperm or eggs in mammals. Most edible mushrooms are the fruiting bodies of fungi classified as Basidiomycetes. Morels and most culinary truffles (such as those in the genus *Tuber*) are members of the Ascomycetes, however. These two major branches of fungi are named after the type of structure (basidia or asci) where meiosis occurs and the sexual spores are formed. For instance, with matsutake, chanterelles, and boletes, basidia are found on the sides of the gills, covering the ridges under the cap, or inside the pores under the cap, respectively. In morels, asci are found on the surface of the pits in the heads.

Understanding how morel (Ascomycete) reproduction differs from that of most other edible (Basidiomycete) fungi requires a cursory explanation of fungal genetics. Genetic information in the nucleus of each cell resides on DNA molecules called chromosomes. Complex organisms have sets of a certain number of chromosomes; the particular number of chromosomes in the set is usually a trait that is common to members of a shared taxonomic grouping. It has not yet been determined how many different chromosomes *Morchella* has. Each chromosome in the set is different, that is, it has different genes coded along its length than the other chromosomes in the set. In a haploid condition (for instance a sexual spore), each cell nucleus has only one copy of each chromosome in the set. These nuclei are referred to as haploid nuclei. Diploid nuclei have two copies of each chromosome.

In a diploid nucleus, the paired copies of each chromosome are called homologous chromosomes. Homologous means that each of the paired chromosomes has the same genes at the same places along their lengths, but because the genes on each chromosome can differ slightly, the chromosomes are not identical. These slight variations in the genes on homologous chromosomes are called alleles. An example of allelic variation of a gene would be different alleles of the gene that codes for hair color. A useful analogy is to think of the two chromosomes in a pair as two libraries of books (genes). Both libraries contain the same books in the same order on their shelves but the individual libraries (chromosomes) might contain different editions (alleles) of any one book. During meiosis, the diploid nuclear state of the fungus individual is reduced to a haploid state in the sexual spore. In the process, the allele for a particular gene can be derived from either of the paired homologous chromosomes in the parent. Continuing the analogy above, this would

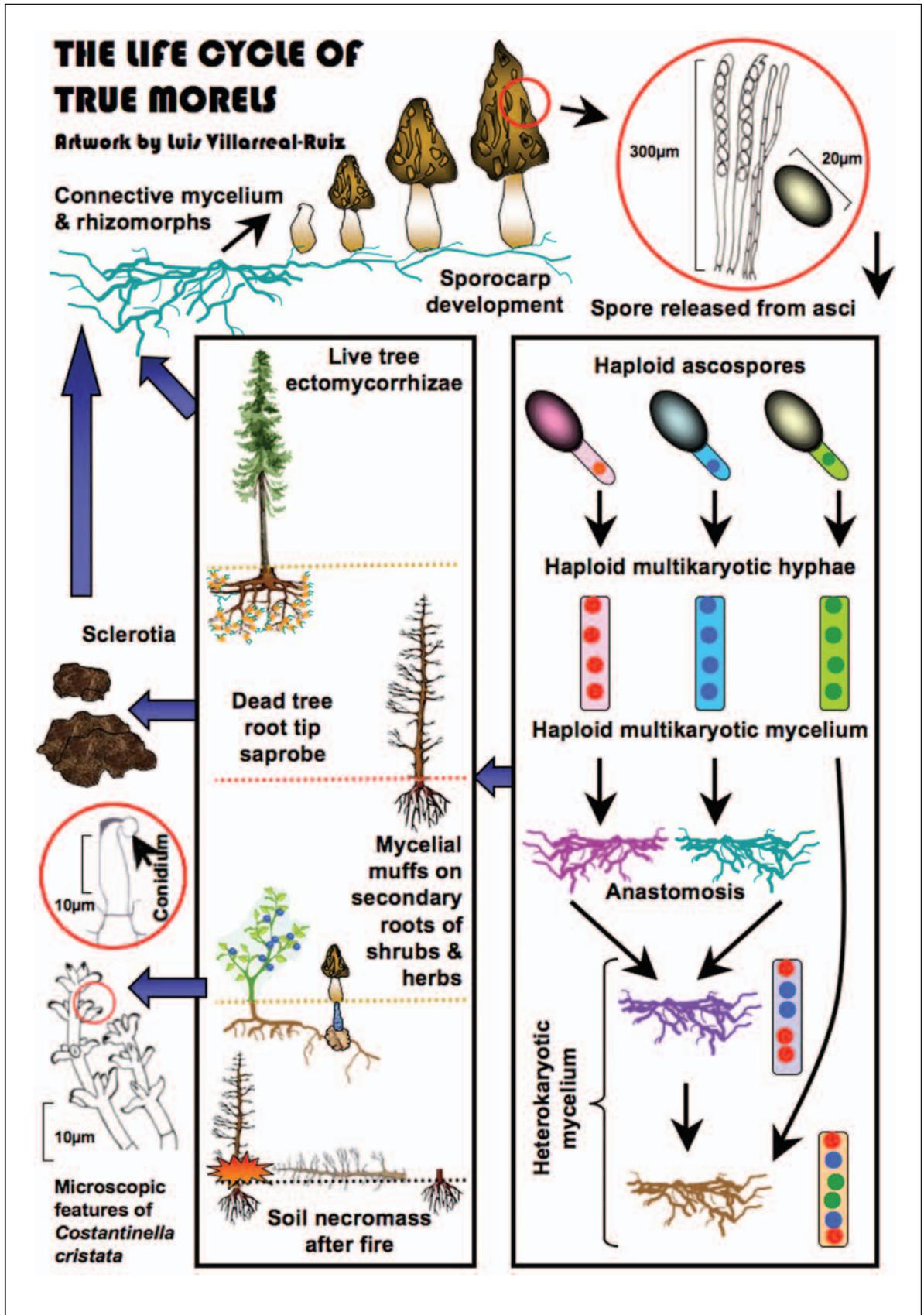
be like creating a new library by photocopying each book, but selecting only one edition from either, but not both, of the original libraries. This reorganization of parental alleles on the chromosomes of the haploid sexual propagules ensures no two offspring receive the same set of alleles on their chromosomes, even if they have the same parents.

Animals and plants are diploid throughout their entire lives because two sets of homologous chromosomes pair up into a diploid nucleus during fertilization. Many fungi, by contrast, can grow for periods of time with only one haploid nucleus (or multiple copies of the same haploid nucleus) per cell. This situation is common when sexual spores germinate and grow for a while in search of other haploid hyphae that are compatible for mating. Fungi do not have genders in the sense of different male and female features, but they do have mating types that must be compatible.

Among Basidiomycetes, a haploid hypha of one mating type typically finds and fuses (anastomoses) with another haploid hypha with compatible mating-type genes. The two compatible haploid nuclei from these fused hyphae just pair up in each cell of the newly formed mycelium without combining to form the single diploid nucleus usually observed in plants and animals. These fungal hyphae are called dikaryotic (Chang and Miles 2004: 58). A karyon is a nucleus containing DNA, so a dikaryon is an organism having two nuclei per cell. In this case, however, the nuclei are haploid, consist of compatible mating types, and are paired. Such cells have the full genetic complement needed to sexually reproduce through the DNA-swapping and chromosome-halving process called meiosis, but the paired haploid nuclei in each cell do not actually fuse for this process until immediately before meiosis begins in the sporocarp.

The nuclear state of a typical morel mycelium, however, is different than many of the mushroom-producing fungi in the Basidiomycetes. Morel hyphal cells have long been observed to have many nuclei per cell. This is called a multikaryotic or multinucleate condition. Recent genetic analysis suggests that, like many Ascomycetes, these are not just multiple copies of the same haploid nuclei, but that many different haploid nuclei co-exist unpaired in the typical morel mycelium. Because the nuclei differ, this is called a hetero-karyotic condition. Morels might also be capable of the highly unusual feat of haploid meiosis. In mammals, the equivalent would be a haploid female growing from an unfertilized egg and then mating with herself to produce offspring. We will discuss the implications of these features for morel reproduction and management later in this section. Morel hyphae also can coalesce to form a number of other interesting structures that we discuss as we come to them (fig. 8).

Morels might be capable of the highly unusual feat of haploid meiosis.



Mycelia—Let us start our examination of the morel life cycle with a germinating sexual spore. Such spores are released from one of the microscopic asci lining the pits in the morel head. Asci are specialized, elongated sac-like cells where sexual spores develop; hence these spores are called ascospores. Morel ascospores have 15 to 30 or more haploid nuclei per spore at maturity (Weber 1988). Thus when an ascospore germinates, the resulting hyphae are already multinucleate or multikaryotic, that is, each cell has multiple copies of the unique haploid nucleus that was formed during meiosis. The linearly arranged cells that form morel hyphae are separated by walls called septa that have pores (Hervey and others 1978, Kendrick 2001). Physiological processes control the passage of cytoplasm (cell contents), nutrients, moisture, and nuclei through these pores. These septa allow researchers to determine how many nuclei exist in each cell. Morel mycelia are almost always multinucleate. They average 10 to 15 nuclei per cell but can range up to 65 (Hervey and others 1978, Volk and Leonard 1990).

The initial haploid hyphae of all sexually reproducing multicellular fungi must fuse with other hyphae (or propagules) containing different haploid nuclei (with compatible mating types) in order to complete a sexual life cycle. Morel hyphae anastomose readily and frequently (Volk and Leonard 1989a, 1990). The result of these frequent fusions among morel hyphae is a heterokaryotic mycelium; that is, many different haploid nuclei coexist in the same hyphae and mycelium (Arkan 1992, Volk and Leonard 1989a). Although heterokaryosis is common in some groups of fungi, it is not common among the fungi that produce most edible mushrooms such as chanterelles, matsutake, or boletes. Stott and Mohammed (2004) stated that heterokaryotic cells are found in the vegetative hyphae, sclerotia, and sporocarps of morels. Volk and Leonard (1990) suggested that there might be pairing of haploid nuclei with compatible mating types within the heterokaryotic mycelium of morels, but such pairing is not as prominent as in fungi that typically

Figure 8 (opposite)—The life cycle of true morels. Ascospores are the sexual spores of morels, resulting from the process of meiosis. They are produced in asci, which are found lining the pits of a morel head. Ascospores are often ejected forcefully from the tip of the asci. They typically contain multiple copies of the same unique haploid nucleus and when they germinate, they form haploid hyphae, also with multiple copies of the same nucleus. The right box illustrates the formation of heterokaryotic mycelia. Among many edible forest fungi, the hyphae from only two haploid spores fuse to form a dikaryotic mycelium. Among morels, additional ascospores (illustrated by green) also can fuse with pre-existing mycelia contributing their unique haploid nuclei to a mix of nuclei in what is then called a heterokaryotic mycelium. We do not know what, if any, limits or constraints there might be to the number of ascospores that can contribute unique haploid nuclei to an existing mycelium, nor whether the types of nuclei present in the hyphae differ among segments of a mycelial network. The left box illustrates the range of potential nutritional substrates that morels seem capable of using. Nutritional preferences could vary by species or environmental circumstances. *Costantinella cristata* is an asexual stage of morel reproduction wherein the hyphae of the morel mycelium form unique structures (conidiophores) to bud off spores (conidia) that include at least one, and possibly more, nuclei from the mycelium. Field and cultivation evidence suggests that sclerotia (tight masses of hyphae thought to store nutrients) can often be an intermediate stage between mycelial growth and fruiting. When morels fruit, the needed nutrients often appear to be translocated by strands of hyphae called rhizomorphs (because they resemble roots).

form paired dikaryons and, significantly, other haploid nuclei continue to co-exist in the same cells. Patterns of anastomosis and heterokaryogamy within and between morel species have not yet been fully investigated, but mycelia of some morel isolates, from putatively different species, appear not to anastomose (Volk and Leonard 1990).

Heterokaryosis in morels has several significant implications, even though the actual expression of these possibilities in nature is not well understood (Kaul 1997). For instance, the haploid hypha from a germinating ascospore does not necessarily have to search for another haploid hypha of a compatible mating type to form a dikaryotic mycelium. It might be able to simply fuse with an established heterokaryotic morel mycelium and contribute its own genetically unique nucleus to the mix of heterokaryons already in the mycelium. The heterokaryotic nature of morel mycelia might also confer adaptation to a broader range of ecological and environmental conditions (Buscot 1992b) because such mycelia have more genetic diversity than those with only two paired haploid nuclei. If hyphae from germinating ascospores can and do indeed fuse with existing mycelium, this could confer the potential for continuous variation and adaptability (Kaul 1997) in response to environmental fluctuations (for instance, episodic droughts) or trends (such as changes in soil chemistry as a forest matures). Additionally, having a variety of alleles of each gene (on the various haploid nuclei) might mask the effect of deleterious mutations because there is a greater probability that a good copy of the gene exists than if the mycelium were only dikaryotic.

**Defining a morel
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Additionally, defining a morel “individual” and its spatial extent in the soil is problematic. For instance, many mushrooms that are classified as Basidiomycetes (such as chanterelles, matsutake, and boletes) form distinct dikaryotic mycelial colonies that can be considered individuals. The structural tissues of all the mushrooms arising from such discrete colonies are genetically identical, so the spatial extent of the colonies can be roughly mapped by analyzing the DNA of their sporocarps. Because morels are formed by heterokaryotic mycelia, no two sporocarps need be alike. Indeed, the mycelium that produces the morel is more like a diverse genetic colony than an individual. Even morels fruiting side by side often appear genetically distinct,¹⁵ and thus are likely composed of different combinations of the multiple haploid nuclei that exist in the mycelium from which they fruit. Therefore the extent of mycelial colonies can only be very roughly mapped by the presence of

¹⁵ Dunham, Susie. 2005. Personal communication. Technical editor, Department of Forest Science, Oregon State University, Corvallis, OR 97331. Preliminary results from analysis of morels collected by Tricia Wurtz in her morel studies near Fairbanks, Alaska.

morels, and if such “patches” of fruiting bodies are in close proximity, it would be difficult to discern whether they are connected and share some nuclei.

The psychrotolerance (Schmidt 1983) of morel mycelia refers to their ability to grow and compete in cold soils. This trait appears to be a common feature among many genera and species in the phylum Ascomycota. For example, Schadt and others (2003) sampled fungal DNA from tundra soils under snow, and of the 125 sampled clonal sequences they extracted, at least one-third were members of the Pezizomycotina, the subphylum of fungi that includes morels. This suggests early adaptation of this fungal lineage to cold environments. In the section “Reproductive Strategies” we will discuss the potential implications of this adaptation to the mass fruiting of fire morels.

The mycelia of some species of morels can produce asexual conidia (Alexopoulos and others 1996). These are produced on and released by simple hyphal structures (conidiphores) and represent a means of clonal propagation. In effect, the mycelium “buds” into spores. No information exists about whether the full range of different nuclei found in a heterokaryotic morel mycelium is transferred into each conidium as it is formed. Individual morel conidia might or might not represent clonal propagation depending on whether all the genetic information in the parent mycelium is replicated in that particular spore. In morels, this conidial stage looks similar to powdery mildew. Because no sporocarps (mushrooms in this case) are produced by such asexual means of reproduction, mycologists working before the advent of genetic analysis often did not know the identity of fungi exhibiting a conidial stage and gave them separate names. In the case of morels, this stage was given the name *Constantinella cristata* by Matruchot (1892), but Molliard (1904a, 1904b) and Constantin (1936) confirmed it to be an asexual reproductive feature of *Morchella* mycelium. Although commonly reported in artificial cultivation, few reports exist of this stage in natural settings. Stamets (2000) reported that in outdoor settings, he only sees it on inoculated sawdust.

Morel hyphae can form a variety of other structures, including sclerotia, mycorrhizae, mycelial muffs, and sporocarps. We discuss each in the following sections. Multiple hyphae can also grow in thick root-like strands called rhizomorphs (literally “root forms”). Rhizomorphs are efficient structures for rapidly transporting large quantities of nutrients or cytoplasm from one location to another and might play an essential role in the rapid formation of fruiting bodies. For instance, morels are sometimes described as emerging from long subterranean stems or various aggregates of hyphae (Philippoussis and Balis 1995, Stamets 2005). These subterranean stems can be connected via rhizomorphs to other structures such as nutrient storage organs (called “sclerotia”) (Philippoussis and Balis 1995) or to mycelial