Two views of Tuber canaliculatum. *Photos: John Plschke III.*

Truffles and False Truffles: A Primer

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Nothing in biology makes sense except in the light of evolution.
—Theodosius Dobzhansky (1900–1979)

Truffles have been the stuff of legend and culinary delight for centuries, even millennia. Historically, all mushrooms have been regarded with mystery or suspicion due mostly to their habit of materializing overnight (completely unlike other "plants") and often in rings (which was clearly the work of dancing fairies). Truffles are curiouser still in that they develop entirely underground. Theophrastus (372–287 B.C.) is credited with the earliest authorship of the group; he considered them the strangest of all plants (you will recall that, until fairly recently, fungi were classified as plants) because they lack any plantlike features, including roots.

When we think of truffles, we hardly get an image of the typical fungus fruitbody, much less that of a mushroom. Not classified with true mushrooms (the Basidiomycetes), the truffles possess sac-like spore producing structures (the ascus; plural asci) and thus are grouped with the morels and cup fungi in the class Ascomycetes.

This begs the question of why any self-respecting fungus would want to produce a fruitbody as hideous-looking as that of a truffle. To most of us, elegance in the fungal world would look more like the Amanitas, Lepiotas, or chanterelles. Something with a stem and a cap, at the very least. Truffle-like fungi look and grow more akin to a potato tuber. (In fact, *Tuber* is the name of the genus of the most highly prized species of truffles.) As with everything in nature, though, there is a reason.

Form follows function: the convoluted hymenium

Although it may not be obvious upon first inspection, species of truffle are most closely related to members of the order Pezizales, which includes *Peziza*, the eyelash fungus (*Scutellinia scutellata*), and the beautiful scarlet cup (*Sarcoscypha coccinea*). But how did members of the genus *Tuber* and their relatives go from a flattened morphology and epigeous (above ground) growth habit to highly convoluted and hypogeous (subterranean)? In his terrific book *The Fifth Kingdom,* Bryce Kendrick illustrates the evolutionary sequence from a flattened, above-ground cup like *Peziza* that likely gave rise to fungi that were increasingly convoluted like *Genea.* Taking the reproductive surface layer, or hymenium, and convoluting it allows for more surface area (and more spore production) per unit area of mushroom. Spring mushroom hunters will recollect a similar morphological progression in morels (*Morchella* species), from their close relatives like *Gyromitra, Helvella,* and *Verpa.* Now take the loosely convoluted *Genea* and increase the infolding, compressing it, and even letting it develop entirely underground. You are beginning to see the intermediate species

Left: Tuber cf. gardneri; *right:* Tuber lyonii. *Both found on NAMA Foray 2005. Photos: John Plischke III.*

en route to the genus *Tuber*. And in nature, a good idea like the truffle-like habit has evolved more than once! There are truffle-like members of the primitive fungal class Zygomycetes, and false-truffle species likely have evolved several different times within the Basidiomycetes.

The class Basidiomycetes is without a doubt the group of fungi most familiar to everyone as it includes the true mushrooms, boletes, polypores, shelf fungi, bird's nests, stinkhorns, and puffballs. Despite the amazing diversity of fruitbodies, all share a common style of spore production: the club-shaped basidium. And with such a diverse array of fruitbody morphologies, it should come as no surprise that within many groups of Basidiomycetes, there are many sequestrate (those with closed or "hidden" hymenia) and hypogeous species. In fact, for just about any common genus of mushrooms, we could follow an evolutionary progression from "typical" mushroom morphology to more and more truffle-like. These are the so-called false truffles. Take *Lactarius*. We know it to be the ancestor of *Arcangeliella* and its most truffle-like kin, *Zelleromyces*. Within the family Boletaceae, *Boletus, Suillus,* and *Leccinum* have all given rise to epigeous sequestrate forms (*Gastroboletus, Gastrosuillus, Gastroleccinum*) as well as false truffles (*Alpova, Truncocolumella,* and *Rhizopogon*). Ditto *Russula* through *Macowanites* to *Gymnomyces*. In fact, no fewer than 14 families of mushrooms have separately given rise to sequestrate or false truffle forms. For an excellent review of the topic, try to find "Evolution in action: from mushrooms to truffles?" by Bryce Kendrick (*McIlvainea* 1994, 11[2]: 34–47).

Form follows function: the subterranean hymenium

So, we have discussed—and hopefully made some sense of—the convoluted morphology of truffle-like fruitbodies, but what about the habit of remaining underground? Wouldn't it make more sense to have the spore-producing surface above ground where spores could be dispersed more easily by wind into the environment? For most fungi that we mycophiles encounter—the mushrooms—this is the method for dispersing offspring. Spores are released to the winds whereby chance may favor them with an opportunity to alight on a suitable substrate for growth. Or not. Which is probably why wind-dispersed species produce such vast numbers of spores. (Wind is the method that many species of plants use to disseminate pollen and fruits as well, of course.) But if wind dispersal is so successful (and it is the *modus* for the ancestors of many truffle and false truffle species), why go underground? No one is completely sure, but there are several possible reasons. Perhaps some groups of hypogeous fungi were driven underground by some biotic factor like mycophagy; maybe mushroom-grazing animals simply were consuming too many fruitbodies for that style of reproduction to be successful within that group. More likely it was because of environmental, or abiotic, factors. Most fungi are very sensitive to dry conditions, especially at the time of fruitbody formation. It is probable that as environmental conditions became more arid locally or globally—and it is well known that this has occurred repeatedly in the earth's history—fungi may have been faced with going underground or going extinct. You may be surprised to learn that many of the deserts of Africa and the Middle East abound with truffle-like fungi! (An in-depth discussion of desert truffles is beyond the scope of this primer, but papers by two of the world's experts on the subject can be found elsewhere in this issue of FUNGI.)

Producing spores within a subterranean fruitbody presents new challenges: namely, how to get those spores dispersed into the environment. To ensure successful spore dispersal, all you have to do is entice a suitable vector. Offers of nutrition would likely work; many plants employ this technique (think nectar, here). All sorts of organisms are known to feed on truffles. Several mammals dig up and consume truffles, including deer and squirrels; some people believe the western red-backed vole feeds exclusively on truffles. Many invertebrates are truffle feeders, including slugs and insects; many fly species probably are strict truffle feeders. (Easily the best source of information on the subject is the brand new book *Trees, Truffles, and Beasts,* reviewed in this issue.) The most advanced plants mimic an animal's own reproductive pheromones, all but guaranteeing pollination. Likewise, it is well supported that truffles attract mammalian vectors by producing odors that mimic reproductive pheromones. According to *The Fifth Kingdom,* species of *Tuber* produce a compound called alpha-androstenol. This chemical also is found in the saliva of rutting boars and acts as a pheromone to attract sows. Many other mammals probably also produce this pheromone, which explains the attraction numerous digging mammals have for these fungi. (Kendrick's book also contains interesting accounts of how pigs and dogs are used for truffle hunting in Italy and France, as well as haggling for the best price in the markets at harvest time.)

North American truffles

You certainly don't have to travel to Europe to find your own wild truffles. There are species of *Tuber* (as well as many kinds of false truffles) that are native to North America. Most noteworthy of the American species are *Tuber gibbosum* and *T. oregonse,* respectively, the spring and fall Oregon white truffles. Of American species, the Oregon white truffle is considered superior in flavor and aroma, even revered by some to be in the same league with the world-famous European truffles: the white Piedmont truffle of Italy (*T. magnatum*), the summer truffle (*T. aesitivum*), and the black Périgord truffle of France (*T. melanosporum*). Although expensive, the Oregon white truffle commands nowhere near the price of its three European cousins (for which you might easily pay $1,000 per pound but up to $3,000 for prized specimens). Historically, the lackluster quality of some of the Oregon truffles harvested, as well as a dearth of knowledge as to how best to store and prepare these species, has left consumers unimpressed and kept prices low, in turn resulting in still more harvesting of lower-quality specimens in order for the harvesters to make a living. But this negative feedback loop is beginning to change, thanks to the efforts of a few passionate advocates like Jim Wells of Oregon Wild Edibles and Charles Lefevre of New World Truffieres. The annual Oregon Truffle Festival showcases the potential of our native truffle species by world-class chefs in a black-tie setting. (See their ad, as well as the article by Charles Lefevre, in this issue for details.)

Along with *T. gibbosum,* most species of American truffles are known from the Pacific Northwest where commercial collectors as well as members of truffle clubs ply the forests, churning up the leaf litter in search of these prized delicacies. Much less famous are the truffle species that occur outside the Pacific Northwest. In North America truffles and false truffles can be found in just about any woodland habitat (as well as some deserts). The brand-new *Field Guide to North American Truffles* by Trappe, Evans, and Trappe (reviewed in this issue of FUNGI) will be invaluable to those wishing to seek out truffles from the wilds. Those authors would be quick to note, however, that not all species found will be palatable. For example, species of the inedible *Elaphomyces,* including *E. granulatus,* are the most widespread of all truffles in North America. But some certainly are worth the effort. First discovered in Texas, *Tuber lyonii* (=*T. texense*) can be found wherever oak trees are growing from Mexico to Ontario and west to the Great Plains. In the Southeast it is commercially harvested from pecan groves (where it is called the "pecan truffle") for use in local restaurants.

Coming soon to a backyard near you: Périgord truffles?

Throughout the more temperate regions of North America it is possible to grow your own truffles at home—including the legendary "black diamond" of Périgord. In fact, someday in the near future domestically produced black diamonds may even be as common as several other types of commercially cultivated mushrooms. It was not that long ago when fresh shiitake and oyster mushrooms began to appear in the markets and grocery stores across North America.

The company New World Truffieres sells seedlings of oak and hazelnut trees that have been inoculated with European species of truffle fungi. Don't have much of a backyard? Why not try growing your truffle trees in containers! See our own Home Cultivator in this issue for details. Note that while the truffle host tree may tolerate severe winter conditions, the fungus may not. If you experience temperatures near zero degrees (F), your region may be too cold. Check with New World Truffieres or other suppliers before making a large investment of time and money.