In the widest sense a truffle is any hypogeous fungus, i.e. one fruiting underground. In this sense there are both ascomycete truffles (the true truffles) and basidiomycete truffles (the false truffles - *Rhizopogon* is an example). In the narrowest sense truffles are only the most sought-after edibles in the genus *Tuber*. The word "tuber" has many more meanings, always referring to round thickened structures; potatoes, for instance, are tubers.

My focus here is on the ascomycete truffle literature, covering specifics like the importance of truffles in the diet of flying squirrels and other furry animals, as well as wide sweeping phylogenetic overviews of the real truffles.

As always, my choice of papers is selective and subjective and my purpose is to give you a taste for the different kinds of research going on, rather than attempt to cover everything.

**Early Truffle Research**


The classic paper by A.B. Frank, originally published in German, in 1885, is now available in an English translation by Jim Trappe. Frank was commissioned by the minister of agriculture of Prussia to investigate ways to cultivate truffles. He set out to investigate this and realized that almost all forest trees that he examined had a fungal mantle on their roots, wherever they were growing. He meticulously looked at trees in various parts of the country, on different soil types, on different slopes etc., but all had this fungal growth. He puzzled over the function of this fungal component and hypothesized that the plants were giving sugars to the fungi and that the fungi supplied the tree with nutrients, especially nitrogen. It took a long time to prove him right, and his paper with its conclusions were ignored for many years. The term mycorrhiza, i.e. fungus root, was coined by him in this paper.

Trappe places his work in the context of the time and the situation he was working in. Both articles are a fascinating read and remind us how recent the discovery of mycorrhiza is, although now we can hardly imagine a time when no one was aware of this mutualism.

**Truffle Classifications**


An excellent start to get a grip on the systematics of truffles is an article by two Danish authors. They comprehensively treat all asco truffles, which are defined as those Ascomycetes whose fruitbodies develop under or just on the soil surface and whose spores are not actively shot off. Real truffles in the genus *Tuber* belong here, along with many others. In the past they all were lumped together in the order *Tuberales*, but now it is established that the shape and way of life of the truffle fruitbody has evolved independently in different families multiple times. The authors show this by using species in the *Pezizales*, a large order that includes both hypogeous (fruiting underground) and epigeous genera (fruiting above ground). They found that many hypogeous genera were more closely related to epigeous genera than to other hypogeous ones.

All the truffles except one species are ectomycorrhizal. The New Zealand species *Paurocotylis pila* is the exception; it forms orange-red fruitbodies that lie on the soil surface, mingling with and resembling the fruits of the non-ectomycorrhizal Podocarp trees towering above them. In New Zealand the only indigenous mammals are seals and a bat, so in the absence of small mammals, it is presumed that the fungus is dispersed by birds. Interestingly, *Paurocotylis pila* has been introduced into the northern parts of the U.K., and is thriving in the barren Orkney Islands, north of Scotland, where it fruits in kitchen gardens and other man-made habitats in the midst of winter. How it ended up there is still a riddle, but perhaps one tourist who had picked up some of those red “fruits” and scattered them in his garden might have been the source.

Zooming in on the genus *Tuber*, the true truffles, is the article by Jeandroz et al. This genus is widespread in the northern hemisphere, but absent from the southern parts of the globe. The
sampling for their phylogeny and biogeographic analyses is focused on Europe and Asia, and most species from North America are left out (Greg Bonito, a graduate student in the lab of Rytas Vilgalys at Duke University studies the North American species). The two classifications, one based on morphological characters and the other on molecular data, do not completely agree, and some modifications of the old system are proposed. An origin for the genus in Europe or Eurasia with subsequent dispersal toward North America over the land bridges, which were present during the Tertiary, is the likely scenario based on the present data.

**Distribution Patterns and Humans**


The activities of man may disturb the original distribution patterns in a major way. Not only do truffles grow now in places like New Zealand and Argentina, where they are not native, but experiments have been conducted to see whether they will grow with tree species other than those with which they associate in their habitats. Not only do truffles grow now in places like Italy, but in Chile there are no oaks. If one wants to grow truffles, one must either import oaks or try to grow them with local trees. Two species of the southern beech (*Nothofagus*) were inoculated, under stringent lab conditions, using limed soils (natural soils in Chile have a pH which is lower than the truffle is used to), and the experiment succeeded with one of the two tree species. The experiment may even be repeated in nature as part of a reforestation project. I am concerned that the introduced species will replace the local species growing with *Nothofagus* and change the checks and balances present in its native community.

But perhaps the risk is not that big. *Tuber melanosporum* is not known for its aggressive competitive behavior; on the contrary, it is easily out-competed when planted in truffle orchards. In northern Italy it is now threatened by an invasive truffle species, *Tuber indicum*, which was introduced as fruitbodies from Asia, despite the fact that Italy had prohibited the sale of that species. The two species are closely related and even look very similar. *Tuber indicum* is harvested on a grand scale in China mainly for export, but for Italian noses, at least, it is not as exquisite as the European species.

Eucalypt plantations are now found everywhere in the world where the climate is right, but these trees also need their own set of mycorrhizal partners. These include hypogeous species, such as *Hydnangium carneum*, a relative of *Laccaria*, a species that has been found from California through Asia to northwest Europe. In New Zealand, it grows with the Eucalypts, but in some places is invading native habitats, and forming ectomycorrhizae with local tree species.

**New Species in North America**


The dry oak savannas and woodlands of southern Oregon and the foothills of the California Sierra Nevada turn out to be a long mother lode for truffles and other hypgeeous species. A series of papers describes several new species and even a new genus, *Gilkeya*, named in honor of an earlier truffle specialist. These up-to-now mycologically neglected areas clearly deserve attention, and the species there, though not very showy, are definitely playing an important role in the ecosystem.

Another new species was described from Rich Balsley’s property in New Jersey where he carefully monitors all fungi and, when needed, calls on experts in the difficult groups to help with identification. Now, his name lives on in the name of the new species *Genea balsleyi*.

**Squirrels and Other Furry Animals**


The first time I saw a big bolete hanging in a bush in the Canadian Rocky Mountains, I thought it weird that someone would put it there; then I saw a squirrel carrying another bolete. Since then, of course, I have frequently seen squirrels eating mushrooms, digging for truffles, carrying Russulas in high trees, etc. The dry forests of the American West harbor a wide variety of truffles, real and false (see above), and the fungi depend on all kinds of rodents to disperse their spores. Rodent scat is so full of spores that in some cases it is hard to see the difference between rodent scats and a fruitbody. You wonder what the animals get out of eating the fruitbodies!

The Northern flying squirrels of the Alberta foothills eat truffles in the summer and use the stored fruitbodies of epigeous mushrooms for their winter supplies. Acorns and truffles both get schlepped around by mice and voles, resulting in an evenly distributed oak coverage. And in the Oregon dunes deer serve to disperse Rhizopogon spores and facilitate the germination of pine seeds in new places.

The flip side is that hypogeous fungi make up a substantial part of the ectomycorrhizal community in many different forests of the dry west.


Umbria, the Italian region in which lie places such as Assisi (home of Saint Francis) and Spoleto, is the heartland of Italian truffle culture. All products originating there and containing truffles scrupulously provide not just the Latin name, but the author of the name. You can see it here in California, where imported truffle oil lists *Tuber melanosporum* Vitt. as one of the ingredients. Truffles are big business in Italy and France, so there is a corresponding wealth of scientific truffle literature. The article by Mello et al. summarizes some of the latest findings—both historical, about the route truffles and their oak partners took to their present distribution areas, after the last ice age, and ecological, about the other fungi present at the tree roots in truffle habitats.

Many questions are still wide open; for instance, it is not understood what triggers fruitbody formation, how the fruitbodies are actually formed, how competitive the truffle species are nor what roles other organisms play in the life cycle of these cryptic organisms.