Snowbank Fungi Revisited

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Abstract

The snowbank fungi are a taxonomically and ecologically diverse group of fleshy fungi that include both Basidiomycota and Ascomycota adapted to the unique microclimate provided by remnant snows in high-elevation conifer forests. This article is a brief review of what is known of the snowbank fungi that occur in western North America.

Key words: fungi, mushrooms, snowbanks, western North America, cold climates

Introduction

One of my first encounters with the "snowbank fungi" was glissading down a snowy slope, when suddenly just before I hit bare ground, hordes of shiny gray mushroom heads appeared unexpectedly from the snow glistening in the high elevation sunlight. It quite took my breath away.

Later I learned that deep in the high-elevation forests of western North America where snowbanks linger long into summer months, a unique group of macrofungi flourishes on the melt waters released by the white remnants of winter. Fruiting bodies initiate in the subnivean zone and push up through the snow as it melts around them forming small caverns. At the snow-soil interface temperatures hover around freezing. As warm air and sun reduce the snowbanks, an array of mushrooms and cup fungi is revealed along margins in the adjacent melt-water zone. As the season progresses they remain as silent sentinels marking the outline of defunct snowbanks with their bodies.

The snowbank fungi are a consistent feature of high elevation western conifer forests in spring and early summer. They are reported primarily from the Rocky Mountains and Cascade Range, but their distribution stretches from southern Canada to northern New Mexico at elevations of 1500 to 3800 m. I have observed them en masse in Colorado, Idaho, Montana, Wyoming, and Canada, and they are well known in the Pacific Northwest, the Sierra Nevada range of California, and the Wasatch Mountains of Utah. Many of the snowbank fungi are endemic to western North America. Others also occur outside the West but not in this unique ecological niche. Moser (2004) states "we have nothing comparable in Europe."

The "snowbankers" appear to be a unique western North American phenomenon. They are not associated with the open snow-beds of arctic and alpine habitats, nor are they associated with glaciers. They are not the typical spring mushroom flora, although a few overlap chronologically with this group. They have not been reported from the eastern USA as an ecological group.

The snowbank fungi are well-distributed where certain conditions are met. They proliferate in regions of high elevation with short, cold summers where snowbanks remain until July. Sufficient elevation is necessary for a deep snowpack in mature forests suffused with downed logs and abundant litter and woody debris. Spring and summer nights must be cool enough to retain the snowbanks, and days warm enough to provide melt water for the fungi which fruit as the soil warms and dries. The fungi can occur on steep slopes or level ground, but snowbanks persist longer on northern slopes and in deep shade where fruiting is protracted. Fruiting can stretch into July and August at higher elevations. The snowbank fungi are associated mostly with the spruce-fir zone (mixed conifers), and particularly with Engelmann spruce (*Picea engelmannii* Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and lodgepole pine (*Pinus contorta* Laud.), although they also occur in mixed whitebark pine (*Pinus albicaulis* Engelm.) forests. It is this particular set of trees that provides enough shade to protect against a quick snowmelt (unlike larch or other deciduous trees at high elevations). These trees are also associated with the mycorrhizal "snowbankers" such as certain species of *Hygrophorus* and *Cortinarius* and they provide woody substrates for the saprobic species as well.

A Brief History

This taxonomically diverse group was first reported as an ecological assemblage by Wm. Bridge Cooke in a 1944 article (Cooke, 1944) on the fungi of Mount Shasta, California. This was followed by *Subalpine fungi and snowbanks* (Cooke, 1955) where he related the details of the macrofungi consistently fruiting near snowbanks in spring. The names of the fungi he reported are out of date (but recognizable). This set of fungi was subsequently called the "Snowbank flora" by Alex Smith in *A Field Guide to Western Mushrooms* (1975). He reported particular species near snowbanks in Idaho where he spent summers, but did not treat the group as a whole in an article. In 1965 Orson K. Miller, Jr. contributed the brief but informative *Snowbank Mushrooms in the Three Sisters Wilderness Area* (Miller, 1965). Both Smith and Miller described several new species of "snowbank mushrooms" and linked additional taxa to

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Table 1. Snowbank-associated fungi in the western USA and their ecology.

BASIDIOMYCOTA	
Gilled Mushrooms (dark or pink spores)	
Cortinarius ahsii	mycorrhizal with conifers
Cortinarius auchmerus	mycorrhizal with conifers
Cortinarius clandestinus	mycorrhizal with conifers
Cortinarius croceus	mycorrhizal with conifers
Cortinarius "flavobasalis" nom. prov.	mycorrhizal with conifers
Cortinarius "flavoroseus" nom. prov.	mycorrhizal with conifers
Cortinarius subalpinus nom. prov.	mycorrhizal with conifers
Cortinarius (*Phlegmacium*) spp.	mycorrhizal with conifers
Entoloma sp.	terrestrial
Nivatogastrium nubigenum	on wood
Gilled Mushrooms (white spores)	
Clitocybe albirhiza	terrestrial decomposer
Clitocybe glacialis	terrestrial decomposer
Hygrophorus goetzii	mycorrhizal with conifers?
Hygrophorus marzuolus	mycorrhizal with conifers
Hygrophorus subalpinus	mycorrhizal with conifers
Lentinellus montanus	wood decomposer
Melanoleuca angelesiana	unknown
Mycena overholtsii	wood decomposer
Neohygrophorus angelesianus	unknown
Strobilurus albipilatus	conifer cone decomposer
Strobilurus occidentalis	conifer cone decomposer
Non-gilled	
Pyncnoporellus alboluteus	wood decomposer
Tyromyces leucospongia	wood decomposer
Jelly Fungi	
Guepiniopsis alpina	wood decomposer
ASCOMYCOTA	
Caloscypha fulgens	seed pathogen on *Picea*
Discina perlata	terrestrial decomposer
Gelatinodiscus	on yellow cedar litter: *Callitropsis nootkatensis;* syn.: *Chamaecyparis nootkatensis*
Gyromitra montana	terrestrial decomposer?
Sarcosoma latahense	terrestrial decomposer?
Sarcosoma mexicanum	mycorrhizal with spruce?
Plectania nannfeldtii	decomposer *Abies*, *Picea* litter

Hygrophorus goetzii. Photo by Steve Trudell.

western snowbanks in a number of publications (references at end). Ammirati and Moser joined in to help delineate snowbank *Cortinarius* taxa, an ongoing process. More recent literature has updated the nomenclature (Bessette et al., 1995; Miller and Miller, 2006; Redhead et al., 2000).

Moser described the snow-bank fungi as a uniquely North American phenomenon (2004). This insight brings with it the realization that the snowbank fungi are dependent on a particular habitat limited to forest-covered mountain slopes with special climatic, geographic, and biological components. These restricted ranges are directly (habitat reduction, forest thinning, fire) and indirectly (global climate change) impacted by human activities.

The Snowbank Fungi

The snowbank fungi are a taxonomically and ecologically diverse group of fleshy fungi that include both Basidiomycota and Ascomycota adapted to the unique microclimate provided by remnant snows in high-elevation conifer forests (Table 1). *Hygrophorus* and *Cortinarius* species are mycorrhizal genera and have a mutually beneficial relationship with conifer trees. Other fungi are saprobic and decompose logs, twigs, cones, and organic debris, except for *Caloscyphe fulgens* which is a seed pathogen.

Gilled Snowbank Mushrooms

All snowbank species of *Hygrophorus* are endemic to North America, with the exception of *H. marzuolus* which is reported from Europe in spring but not necessarily with snowbanks (Moser, 1955). *Hygrophorus* species can initiate fruiting in the subnivean zone and *H. goetzii* has been observed under 7–10 cms of solid ice where snow has melted and refrozen (Miller, 1965). *Hygrophorus goetzii* has a small viscid pinkish-cream fruiting body (Hesler and Smith, 1963; Miller, 1965; Miller, 1967). *Hygrophorus marzuolus* (Fr.) Bres. and *H. caeruleus* O.K. Mill. have large, fleshy bluish-gray sporocarps, but only the latter has a strong smell of rancid meal (Miller, 1984; Bessette et al., 1995). *Hygrophorus subalpinus* A. H. Sm. is a robust pure white mushroom with a gelatinous veil at first, and is sold in markets as an edible in the Pacific Northwest. *Neohygrophorus angelesianus* (A. H. Sm. and Hesler) Singer combines the macro-features of *Hygrophorus* and *Clitocybe*, and produces small brownish-gray mushrooms with drab purple brown tints and decurrent gills; the red reaction of fresh gill and stem tissue to KOH is distinctive (Smith and Hesler, 1942; Miller, 1965; Miller, 1967; Bessette et al., 1995).

Several species of *Cortinarius* are associated with snowbanks (Miller, 1965) and others occur later in the spring grading into the typical spring mushroom flora. *Cortinarius ahsii* McKnight first described by McKnight is a nondescript brown mushroom with a bright yellow veil named for Alexander H. Smith (his initials: A.H.S.);

Hygrophorus subalpinus. Photo by Steve Trudell.

it is likely synonymous with *C. zinziberatus* (Fr.) Fr. or *C. colymbadinus* Fr. of Europe which are not reported with snowbanks according to Moser. While *C. ahsii* became a well-known "snowbanker," it is often not the most common snowbank *Cortinarius* species. Subsequent study by Ammirati, Moser and Miller revealed at least two other look-alikes that fruit at the same time that can be sorted out with the help of a UV light. This includes "*C. flavobasalis,*" which fluoresces orange at the base (fresh young fruiting bodies!), and "*C. flavoroseus,*" with a veil and flesh (cut it open) that fluoresce bright yellow. The latter two species have provisional names and are currently under study for publication. Ammirati states that a number of the snowbank *Cortinarius* subgen. *Telemonia* are not named, and Moser notes that particular *Cortinarius* species from subgenus *Phlegmacium* can also be present. Out of four new taxa of the genus *Cortinarius* dealt with in Moser (2002), at least one (*Cortinarius auchmerus* M.M.Moser) might be associated with snow banks. Occasionally, particular *Entoloma* species are reported next to snowbanks in spring.

Two of the most common snowbank fungi, *Clitocybe glacialis* Redhead, Ammirati, Norvell and M.T. Seidl (=*Lyophyllum montanum* A.H. Sm.) and *C. albirhiza*, are considered decomposers. *Clitocybe glacialis* is recognized by its overall silvery gray color, which glistens in sunlight reflected off snow (Smith, 1957; Smith, 1975; Miller, 1967). *Clitocybe albirhiza* H.E. Bigelow and A.H. Sm. is a related rather nondescript pale brown mushroom of the same size that can be recognized by the copious white subterranean rhizoids at its base (Bigelow and Smith, 1962). Mushrooms of both emerge from the subnivean zone, and persist after the snow has melted, likely due to slow decomposition in a cool climate. Interestingly, as they decompose, the two species become difficult to distinguish as both become a watery yellow-brown.

Mycena overholtsii A.H. Sm. and Solheim fruits in clusters on decorticated logs buried in the snow (Smith, 1979). As snow recedes around the log, the mushrooms mature in moist snow chambers. The long, hirsute stipe is often buried in deep cracks in the woody substrate. It is recognized by its rather large size for a *Mycena*, a gray-brown striate bell-shaped cap and substantial mycelium on the lower part of the stem. Hence the common name "fuzzy foot." Other early species of *Mycena* are typically much smaller. *Lentinellus montanus* O.K. Mill. is another agaric found on logs near snow, but here the brown shell-shaped caps lack a stem. *Melanoleuca angelesiana* A.H. Sm. is characterized by a gray-brown

Mycena overholtsii. Photo by Steve Trudell.

Lentinellus montanus. Photo by Steve Trudell.

Mycena nivicola nom. prov. B.A. Photo by Steve Trudell.

Nivatogastrium nubigenum. Photo by Steve Trudell.

Caloscypha fulgens. Photo by Steve Trudell.

Gyromitra montana. Photo by Steve Trudell.

pileus, contrasting white gills and a dark stipe (Smith, 1944; Bessette et al., 1995). It fruits on the ground near snowbanks and in other habitats as well. *Melanoleuca* species have a white spore print and amyloid ornamented spores (somewhat similar to those of *Russula*). Macroscopically they often have a "twisted-striate" stipe. Two western *Stobilurus species* fruit in early spring near snowbanks, *S. albipilata* (Peck) Wells and Kempton and *S. occidentalis* Wells and Kempton, and they are delineated on microscopic characteristics (Redhead et al., 1980). Both are tiny collibioid mushrooms and it is helpful to follow their long stems down to buried cones for confirmation of identification. Although not strict "snowbankers," they do occur at the same time and in the same habitats. All of the species in the preceding five genera (*Clitocybe*, *Mycena, Lentinellus*, *Melanoleuca* and *Strobilurus*) have white spores and are North American species.

A Gastroid Snowbank Fungus

Nivatogastrium nubigenum (Harkn.) Singer and A.H. Sm. is a unique gastroid fungus related to the genus *Pholiota* (Singer and Smith, 1959; Miller, 1965). The cap never opens to release the spores and this is hypothesized to be an adaptation to extreme cold and drought. Cooke (1955) reported that squirrels eat the fruiting bodies and disseminate the spores, and he described specimens set out on stones and branches to dry for later use. The caps are often buried in snow and revealed only at maturity. There are no other secotioid fungi known on wood, and this species is restricted to North America. I have collected it near McCall, Idaho, on logs in the spruce-fir zone, and Cooke collected it on Mount Shasta in California. Interestingly, *Nivatogastrium baylisianum* E. Horak has been reported from alpine areas in New Zealand (Horak, 1971).

Non-gilled Snow-lovers

Non-gilled Basidiomycota include several wood decomposers in the polypore and jelly fungus groups. There is some evidence that the hyphal growth of *Tyromyces leucospongia* (Cooke and Harkn.) Bondartsev. and Singer (white sponge polypore) is maximized at 12 to 16 deg. C, and that it can complete its life cycle below 7 deg. C. (Bessette et al., 1995). It is recognized as a white, soft marshmallow-like polypore with angular pores found on downed logs at snowmelt. Many of the snowbank fungi do not grow well in culture and have therefore not been shown to be psychrophilic. The bright orange soft polypore with ragged teeth found in the same habitat is *Pycnoporellus ablboluteus* (Ellis and Everh.) Kotl. and Pouzar (orange sponge polypore). *Guepiniopsis alpina* (Tracy and Earle) Brasf. (lemon drops) is a gelatinous basidiomycete and some jelly fungi are able to sporulate after being frozen while fully hydrated (Ingold, 1982), an adaptation well-suited to cold climates. Miller (1981) cites this as the most prolific species during snowmelt in the western mountains, and we have shown it prefers cold temperatures for fruiting (Cripps, unpublished).

Ascomycetes Snowbankers

Numerous Ascomycetes are associated with snowbanks, and several are reported here, although more certainly exist and particularly where melting snowbanks are combined with burned ground. *Caloscypha fulgens* (Pers.) Boud., an orange cup fungus with a bluish exterior (especially when handled), also occurs in Europe. It is a seed pathogen on spruce (*Picea*) and kills dormant seeds during stratification (cold treatment) in cool, moist soils (Paden et al., 1978). *Sarcosoma mexicanum* (Ellis and Holw.) Paden and Tylutki is a black cup fungus with a swollen gelatin-filled base (Tylutki, 1979) that functions as a moisture reserve during spore maturation. It often fruits with the snowbank flora, but is not a strict snowbank associate. I have observed it in Oregon, Idaho, and New Mexico, and it is reported from western Montana. *Plectania nannfeldtii* Korf fruits in the subnivean zone and the black stalked cups emerge as snow melts in pockets around them (Miller, 1965; Miller, 1967; Seaver and Shope, 1930; Tylutki, 1979). The rubbery ascocarps are remarkably durable and endure long after the snows are gone. It was first described by Swedish mycologist

Plectania nannfeldtii. Photo by Steve Trudell.

Nannfeldt on a visit to Colorado in the early 1900s (Evenson, 1997).

Nivicolous Slime Molds

A set of Myxomycetes (slime molds) are also known to occur near snow. They are more commonly called the "nivicolous" myxomycetes and they are protists not fungi. They have been called the snowbank slimemolds, but "snowbank" is defined in a broader sense for these organisms to include subalpine snowbanks and also alpine snowbeds. Habitats include proximity to snow in alpine, arctic, and high elevation habitats around the world and in the eastern USA. For photos see myxo-specialist Stephenson's website: www.myxoweb.com/snow.htm.

A Last Thought

When collecting snowbank fungi, it is important to record the particulars of habitat and location since this specialized niche is easily overlooked in forest management. If snowbank fungi truly are restricted to the western US and require certain biotic and abiotic conditions, only those who recognize them can provide information on their distribution and identify potential threats. They are worth getting to know for their ecology, their uniqueness, as well as for their beauty.

Acknowledgments

This paper is dedicated to the memory of Orson K. Miller, Jr., a mycologist and wonderful mentor who introduced me to the snowbank fungi by in 1985 when our mycology class at the Flathead Lake Biological Station collected snowbank fungi on the steep slopes to Jewel Basin in western Montana. I had collected them in Colorado for ten years previously, but their import had somehow escaped me. The article "Snowbank Fungi of Western North America: Cold but Not Frozen" reprinted with permission (Botanical Electronic News ISSN 1188-603X, No. 377 April 12, 2007, Adolf Ceska, editor, Victoria, B.C.). I would like to thank Joe Ammirati and Egon Horak for their comments on the first draft of this article and Adolf Ceska for asking me to write it.

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Lachnellula suecica. Photo by Steve Trudell.

Sarcosphaera coronaria. Photo by Steve Trudell.

Neohygrophorus angelesianus. Photo by Steve Trudell.

Mycena nivicola. Photo by Steve Trudell.

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For more on Snow Mushrooms: Just for fun, check out this article that describes mushrooms actually made out of snow!

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