
Dr. A. Ceska, P.O.Box 8546, Victoria, B.C. Canada V8W 3S2

SNOWBANK FUNGI OF WESTERN NORTH AMERICA: COLD BUT NOT FROZEN

From: Cathy Cripps, Dept of Plant Sciences & Plant Pathology, Montana State University, Bozeman, MT 59717 [ccripps@montana.edu]

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.

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 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 & 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. *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 *Caloscypha fulgens* which is a seed pathogen.

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, 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. & 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, 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.); it is likely synonymous with *C. zinziberatus* (Fr.) Fr. of Europe which is not reported with snowbanks according to Moser. While this species 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 which 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 they 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 & 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, 1975; Miller 1967). *Clitocybe albirhiza* H.E. Bigelow & 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. & 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 angelisiana* A.H. Sm. is characterized by a gray-brown 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. albigilata* (Peck) Wells & Kempton and *S. occidentalis* Wells & Kempton, and they are delineated on microscopic characteristics (Redhead et al. 1980). Both are tiny colliboid 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.

Nivatogastrium nubigenum (Harkn.) Singer & 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 are revealed only at maturity. There are no other secotiid 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 Basidiomycota include several wood decomposers in the polypore and jelly fungus groups. There is some evidence that the hyphal growth of *Tyromyces leucospongia* (Cooke & Harkn.) Bondartsev & 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 abloluteus* (Ellis & Everh.) Kotl. & Pouzar (orange sponge polypore). *Guepinopsis alpina* (Tracy & 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).

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

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 link on myxospecialist Steve Stephenson's website <http://www.myxowb.com/snow.htm>.

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.

ACKNOWLEDGEMENTS

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. I would like to thank Joe Ammirati and Egon Horak for their comments to the first draft of this article.

Table 1. Snowbank-associated fungi in the western USA.

Taxa Ecology BASIDIOMYCOTA

Gilled Mushrooms (dark or pink spores)

- Cortinarius ahsii* McKnight mycorrhizal with conifers
- Cortinarius auchmerus* Moser mycorrhizal with conifers
- Cortinarius clandestinus* Kauffman mycorrhizal with conifers
- Cortinarius croceus* (Schaeff.) Gray mycorrhizal with conifers
- Cortinarius "flavobasalis"* McKnight & Moser nom. prov.

mycorrhizal with conifers
Cortinarius "flavoreus" nom. prov. mycorrhizal with conifers
Cortinarius subalpinus nom. prov. mycorrhizal with conifers
Cortinarius (_Phlegmacium_) spp. mycorrhizal with conifers
Entoloma sp. Terrestrial
Nivatogastrium nubigenum (Harkn.) Sing & A. H. Smith on wood

Gilled Mushrooms (white spores)

Clitocybe albirhiza Bigelow & A. H. Smith terrestrial decomposer
Clitocybe glacialis Redhead et al. terrestrial decomposer
Hygrophorus goetzii Hesler & A.H. Smith mycorrhizal with conifers?
Hygrophorus marzuolus (Fr.) Bres. mycorrhizal with conifers
Hygrophorus subalpinus A. H. Smith mycorrhizal with conifers
Lentinellus montanus O.K. Miller wood decomposer
Melanoleuca angelesiana A. H. Smith unknown
Mycena overholtsii A. H. Smith & Solheim wood decomposer
Neohygrophorus angelesianus (A. H. Smith & Hesler) Singer unknown
Strobilurus albipilatus (Peck) Wells & Kempton conifer cone decomposer
Strobilurus occidentalis Wells & Kempton conifer cone decomposer

Non-gilled

Pyncnoporellus alboluteus (Ellis & Everh.) Kotl. & Pouzar wood decomposer
Tyromyces leucospongiosus (Cooke & Harkn.) Bondartsev & Singer wood decomposer

Jelly Fungi

Guepiniopsis alpina (Tracy & Earle) Brasf. wood decomposer

ASCOMYCOTA

Caloscypha fulgens (Pers.) Boud. seed pathogen on _Picea_
Discina perlata (Fr.) Fr. terrestrial decomposer
Gelatinodiscus flavidus Kanouse & A.H. Smith on yellow cedar litter: _Callitropsis nootkatensis_ (D. Don) Oerst.;
syn.: _Chamaecypris nootkatensis_ (D. Don) Spach
Gyromitra montana Harmaja terrestrial decomposer?
Sarcosoma latahense Paden & Tylutki terrestrial decomposer?
Sarcosoma mexicanum (Ellis & Holw.) Paden & Tylutki mycorrhizal with spruce?
Plectania nannfeldtii Korf decomposer _Abies_, _Picea_ litter

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POSTSCRIPT:

Snow Mushrooms

Just for fun, check out this article which describes mushrooms actually made out of snow!

Cornish, V. 1902. On snow-waves and snow-drifts of Canada. *The Geographical Journal* 20:137-173.

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