Peziza nivalis— constant species or species complex?

by Andrus Voitk, Renée Lebeuf, Donald Pfister

Our story begins in the senior author's yard (Fig. 1). The house is in a clearing about 20 m asl, beside a river in a mixed forest on sandy soil in a valley overlying limestone bedrock; the clearing, a mixture of moss, grass and weeds—termed wildflowers by the owners—is mown once or occasionally twice a year, and is not subjected to care, fertilizer, or weed killer. There is a fire pit at the forest edge and a second burn site in the middle of the clearing, placed to avoid igniting tree branches when burning brush. Every year these sites have been surveyed for carbonicolous fungi. Ten years, nothing.

Winter 2019–2020 tarried, but brought record snowfalls at the end of spring, followed by a drawn-out period of intermittent snow through spring thaw. During one of these periods of thaw, small cup fungi, brown like last year's birch leaves, were found on the burn site in the clearing: eight thin brown discs, 7–26 mm in diameter, a few cup-shaped, but most flat (Fig. 2), followed after some intervening snowfalls by a second crop of 5 cups a week later. Pitting of the hymenium seemed characteristic, prompting a review of other collections, which revealed two hitherto unidentified earlier collections, 2002 and 2009, 25 and 60 m asl, 3 and 70 km away from the current site. Both collections had pitted hymenia, were from burnt ground and occurred at snowmelt (Fig. 3). The collection from 2002 was destroyed by mould in 2010 with only a photo remaining, but a robust collection remained from 2009. Because these were the first fungi to arise from the burn site in ten years, because the species had been collected twice before without identification, but mostly because the choice at snowmelt time is limited, a concerted effort was made to identify the species.

How can somebody as blessedly ignorant about cup fungi as the senior author begin to identify these from what seems like tons of other brown cups?

Glossary of Terms

Anthracophilic Coal-liker, or a species that prefers to grow with coal, but the relationship is facultative, not obligate, so that the species may also be found in coal-free sites. From the Greek anthrax (coal) and philia (friendship).

Carbonicolous Coal-dwelling (living/growing in/on/with coal). Suggests an obligate relationship, and inaccurate for a facultative coal-dweller that may also grow on a substrate not containing coal.

Complex Denotes a group of similar, frequently cryptic, related species. Frequently these have been known by a single name until molecular studies have shown an unsuspected evolutionary diversity, often related to geologic dispersal to regions with intervening impediments to continued mixing of genetic material.

Constant English meaning of unwavering or steadfast, not the current favourite, "annoyingly repetitive". Think of le Carré's *The constant gardener*.

Fortoulism Coined by Donadini,[1] a French student of Ascomycetes, to describe the phenomenon of cylindric paraphyses becoming inflated (moniliform) or deformed. He remarked that specimens close to snowbanks (presumably younger) were lighter in colour and had cylindrical paraphyses, but those further from the melting snow (presumably older) were darker and showed strongly inflated and deformed paraphyses. In our QC collection of light specimens close to snow, most paraphyses were cylindrical, whereas in the darker NL specimens fortoulism was flagrant. Hymenial pitting is also presumably due to old age: in the younger QC population it was observed only on one old ascocarp, but all were pitted in the older NL population.

Donadini first observed the phenomenon of inflated, deformed paraphyses, now known to be characteristic of many species of *Peziza*, in *Peziza fortoulii*, a taxon named in honour of French mycophile Gabriel Fortoul, and thus coined the term "fortoulism" to indicate structural inflation. *Peziza fortoulii* was recognized by Pfister[2] as a later synonym of *P. nivalis*.

Gabriel Fortoul studied mycology with the noted French mycologist Pouchet, and later became a pharmacist in Toulon, La Valette du Var. He persisted with his mycophilic avocation, and became a valued guide for many mycologists who came to collect and study the mycota of the region. He was known for painting extraordinary aquarelles, and his wife was renowned for finding rare and unusual fungi, reminding the second author of this tract of the wife of the first author.

Nivaloid Similar to *P. nivalis*, i.e. member of the *P. nivalis* complex. A slightly contracted construction for easier pronunciation.

Nivicolous Snow-dwelling, usually in the sense that the organism thrives when snow is still on the ground, i.e. snowmelt time, or for fungi, the group often known as snowbank fungi.

Well, surround yourself with knowledgeable people. And use books. A great time to test the pictorial key in *Ascomycete fungi of North America* by Beug et al.,[3] reviewed to deserved praise by Dave Malloch in Omphalina.[4] As suspected, the key led to pages of photos of brown cups and discs, most resembling ours, but none with the same pockmarked hymenium (Fig. 2, 3). What if it is not a consistent feature? Two other characters may help to narrow down the field a bit: a preference for an old burn site, and fruiting while snow is still on the ground. This helped a lot. None of the described burn site cups quite fit, but the book also gave a brief review of carbonicolous pezizas not treated there. Among these, *Peziza nivalis* stood out as a species that fruits when snow is still on the ground. Spore size was provided, and the length matched our specimen. What was expected to take at least a full day of hunting, with no big hopes of success, was solved after no more than 10–15 minutes of reading—it was that easy! Thanks, Michael.

Now that we have a putative name for our find, let us see what is known about the species. *Peziza nivalis* has not been known for long and is definitely not common.... unless you read the ASCOfrance Forum, a wonderful website for anybody interested

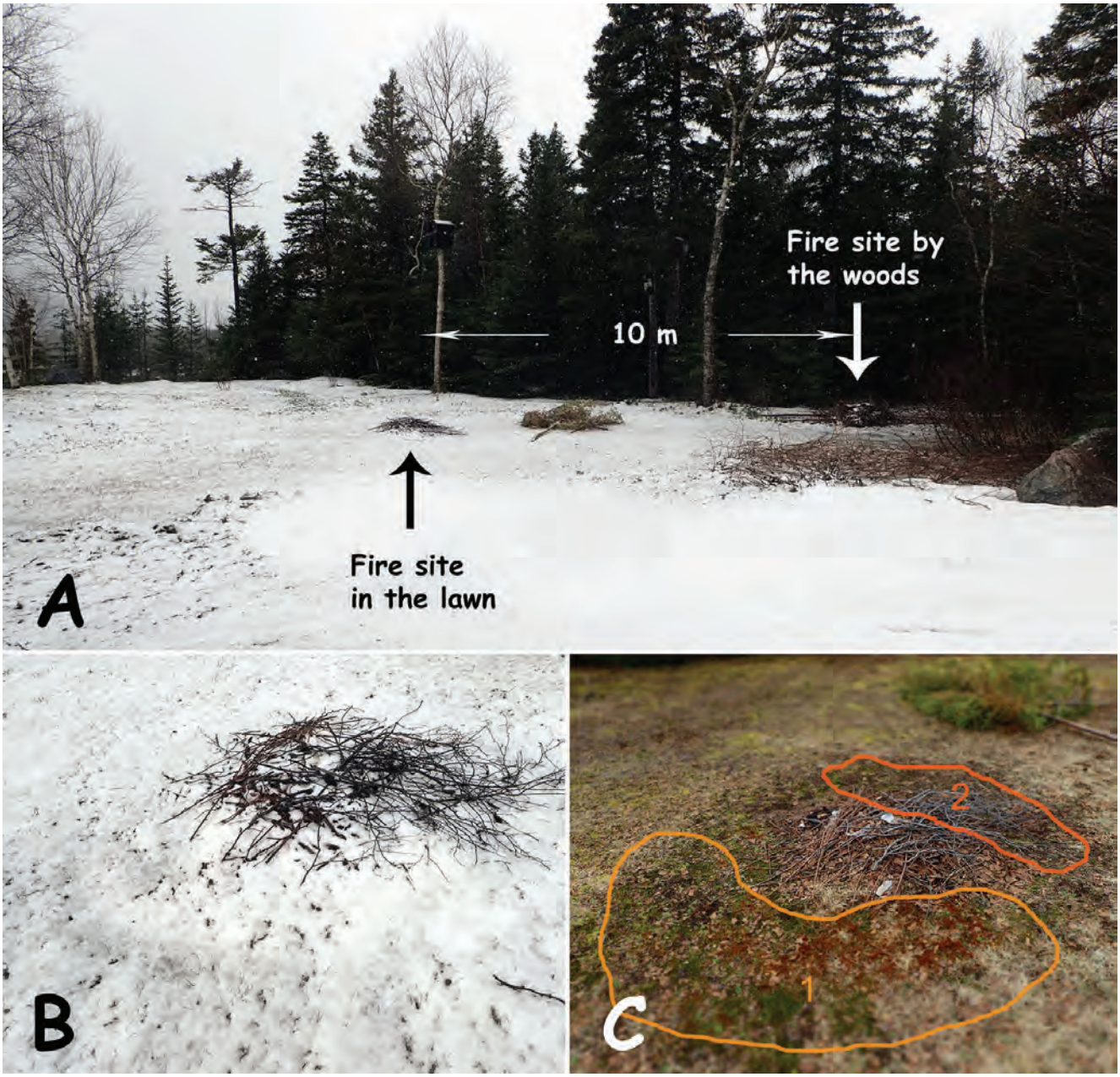

Figure 1: Habitat of current NL collection of alpine snowbank fungi. (A)Senior author's lawn, on the sandy bank of the Humber River, 20 m asl. Two fire sites marked, 10 m apart from each other. (B–C) Close-up view of the fire site in the lawn, two days apart. Orange line 1 in (C) shows location of first crop of the *Peziza sp.* "nivenena", and 2 shows the location of the second crop a week later.

in ascomycetes, where it is described as "a rather common species in the French Alps when the snow melts."[5] In other words, like many niche organisms, it is generally very uncommon, but quite common in its specialized habitat. First described by Heim and Rémy in 1932 from the French Alps between 2100 to 2400 m asl,[6] it has since been described as an alpine snowbank species from other mountainous areas around the globe: Australia, Austria, Bulgaria, Canada (BC), Israel, Italy, Montenegro, New Zealand, Norway, Switzerland, and the USA (CA & OR). There is no formal report of the species from eastern North America, but Renée Lebeuf, one of the authors, posted photos on the Mycoquébec website of a 2017 collection from her flowerbed in Saint-Casimir, Québec, about 30 m asl (title banner).[7]

You may wonder why we consider this lawn and flowerbed denizen from 20–60 m asl as a fit for a species recognized as alpine the world over. One explanation could be the latitude = altitude theory from the previous article, the theory justifying the term arctoalpine: species that like the cold temperatures found at high altitudes also enjoy cold in arctic latitudes without the need for high elevation. By itself, that theory is not solid here, because being

Figure 2: *Peziza sp.* "nivenena". (A) Exposed ascocarp of 2020 NL collection after snow has gone. Note several small pits irregularly distributed in hymenium. (B) Same ascocarp immediately after new snowfall has melted, but water not evaporated. The small pits seem swollen shut. (C) 2017 QC collection, in close proximity to melting snowbank. Ascocarps lighter, without pits, presumed to be younger. (D) Abhymenial (lower, outer, sterile) surface. (E) Close-up of cut surface, showing weak layering. Arrow indicates cut through one of the pits: hymenium is missing, but other layers intact.

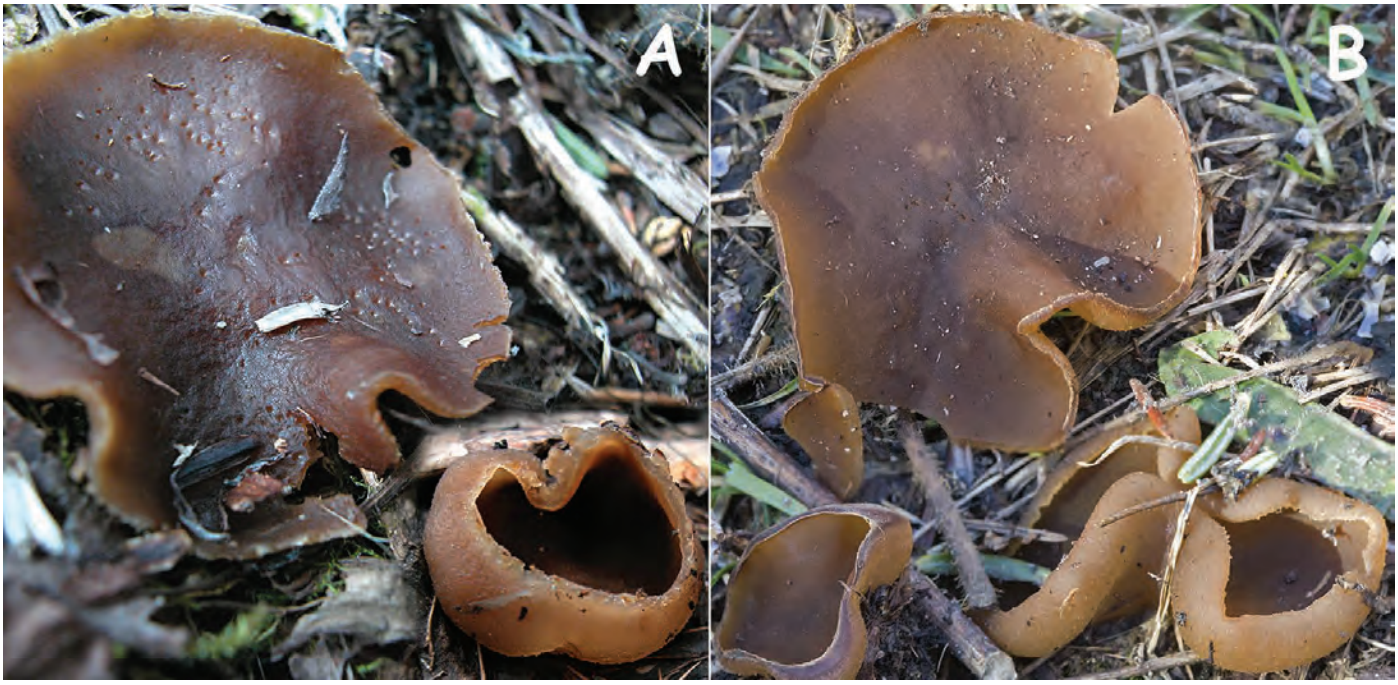

Figure 3: Other two NL collections. (A) Collection from May 17, 2002. Identification based on macromorphology only, as the specimen was destroyed by mould in 2010. (B) Collection from Apr 11, 2009, near Rocky Harbour, NL (70 km away, 57 m asl). Note again characteristic pockmarking of hymenium.

further north than the un-Alaskan USA is not the same as being northern, let alone arctic; we are at the same latitude as Paris. Another explanation we have invoked in some instances adds the effect of sea currents: the cold Labrador Current bathing our shores, makes our climate much more northern than the latitude might suggest, compared to Europe, warmed by the Gulf Stream.[8] This explanation is weakened slightly by Renée's collection, because the climate in her home is not exposed to the Labrador Current, being considerably more continental than ours. As I write these words on the morning of May 8, 2020, there is 4" of fresh snow on the ground outside my window.

It is possible that the important things to this species are first the temperature-moisture conditions found at snowmelt, and secondly the nutrition release created by past fires. If these needs are satisfied, alpine habitat may be an irrelevant red herring imposed by human nature. After all, no sane person walks around looking for little nondescript brown discs on burn sites on oh, so boring soppy muddy lawns in the cold, cloudy, unpleasant weather of April–May, when snow alternates with rain. It is much more exciting to organize a trek to the high mountains in the nice, sunny and warm days of July, there to dally around a pannier of Champagne and caviar while cooling off beside a snowbank, casually exploring the moist drainage areas for unusual fungi. Any find, no matter how pedestrian, is unusual, encouraging future similar surveys, thereby guaranteeing the fungus immediate mountaineering fame. The same phenomenon has been recorded for species like nivicolous slime moulds,[9] an observation we have been able to confirm. The alpine habitat may have nothing to do with the fungus or its needs, but be a fiction pinned on it by us.

An anthracophilic lifestyle was not mentioned when the species was described, or by all observers, but has been noted since.[3,10,11] All three NL collections came from burnt ground, with charcoal evident in the photos. Renée's collection came from a flowerbed in her yard, where there has been no fire. Other species known for their affinity for burnt ground, like fire morels, have been collected on occasion from sites with no evidence of past fire. This could be one such species.

This might be a good time to discuss the pockmarks in the hymenium. Are they a good identification character for the species? In the case of the NL finds, all three collections had pockmarks, and the specimen from the Rockies collected by Pfister also had pockmarks in the hymenium.[2] However, many descriptions do not mention them and produce photos with contiguous hymenia (e.g. the QC collection, Fig. 2C). The small holes go through the

hymenium down to the hypothecium (Fig. 2E), and may be obscured by tissue swelling (Fig. 2A, B), but this cannot explain all the descriptions and photos of smooth hymenia. When found, they can have identification value, but they cannot be considered a sine qua non identification characteristic. Both Renée Lebeuf and Don Pfister believe they are related to age, as both have observed them in older specimens.

As is often the case, several similar species have been described. In 1992 Don Pfister, the third of our authors and a recognized student of Ascomycetes, reported on a find of *P. nivalis* in the California mountains, and used that report to review the nomenclature of these snowbank pezizas, synonymizing several names, and creating a new name, *P. heimii*, for a similar species that differed by having relatively huge spores (27–33 x 15–16 µm).[2] This work, from the tail end of the morphological era, gave the species a very solid taxonomic footing to enter the era of molecular studies. To date the *Peziza nivalis* populations have not been studied with current molecular techniques, although the two sequences from USA (CA & OR), available at the time, were used to place *P. nivalis* within the core species of *Peziza*;[11] to those two, four sequences from New Zealand have been added in GenBank. A superficial look (Fig. 4) suggests that the western North American and the New Zealand collections might form a single species clade. If all nivaloids were to fall into one clade, it would be a species of very unusual genetic stability, without much evolutionary change in response to wide geographic dispersal across both hemispheres. In that case, *P. nivalis* would surely be one of the most constant as well as cosmopolitan of fungal species. Because recent techniques have uncovered so many species complexes, a molecular study of the various reported collections across the globe would be very interesting. The odds probably favour a complex, giving an opportunity to resuscitate some synonymized names.

While we await the post-Covid-19 opening of laboratories to investigate this, we can seek available evidence favouring either nivaloid constancy or complexity. All four eastern Canadian collections may be considered coastal, although one may debate whether the inland portion of the St Lawrence River should be considered coastal. Ergo, it is possible that instead of being lowland versions of the same species, they represent a different species in the complex, one preferring littoral habitats at low altitude. We turned to spore measurements (Fig. 5), to see if they can give a hint, and learned the following:

1. Measurements of the three preserved eastern Canadian specimens are nicely superimposed, supporting conspecificity. They differ from spores from other geographic locations, suggesting ours may indeed be a separate low altitude coastal species.

2. Spores of the type specimen from the French Alps are significantly shorter than any others plotted. If the difference is not due to observer or technique variation, it seems sufficiently diverse to suggest *P. nivalis* s. str. differs from the others shown.

3. Spores of specimens reported from Switzerland are narrower than those from eastern North America. Although the length matches, barring observer or technique variation, average spore size seems sufficiently far apart to suggest species difference, making this at least the third species of the complex from the European Alps (counting *P. heimii*).

4. Spores of all specimens from western North America are significantly broader than those from the east:

    a. Pfister's collection from the California Rockies[2].

    b. Four of five collections with spore measurements from western North America (CO, ID and BC) located on MyCoPortal[12] (the fifth collection was excluded for technical reasons).

    c. *Peziza phaeotheca*, a species described from Utah[13] and synonymized with *P. nivalis* by Pfister.[2]

These speculations are attempts to formulate a big picture from small data. But it is fun, and that is how the science of mycology works: a hypothesis is developed to explain observations in the field and then tested in the lab. The answer is taken back to the field to see if it fits. We shall await the definitive results from molecular studies (see Table 1: DAOM accession numbers for follow-up) to return to the field. Meanwhile, preliminary or not, you heard it here first.

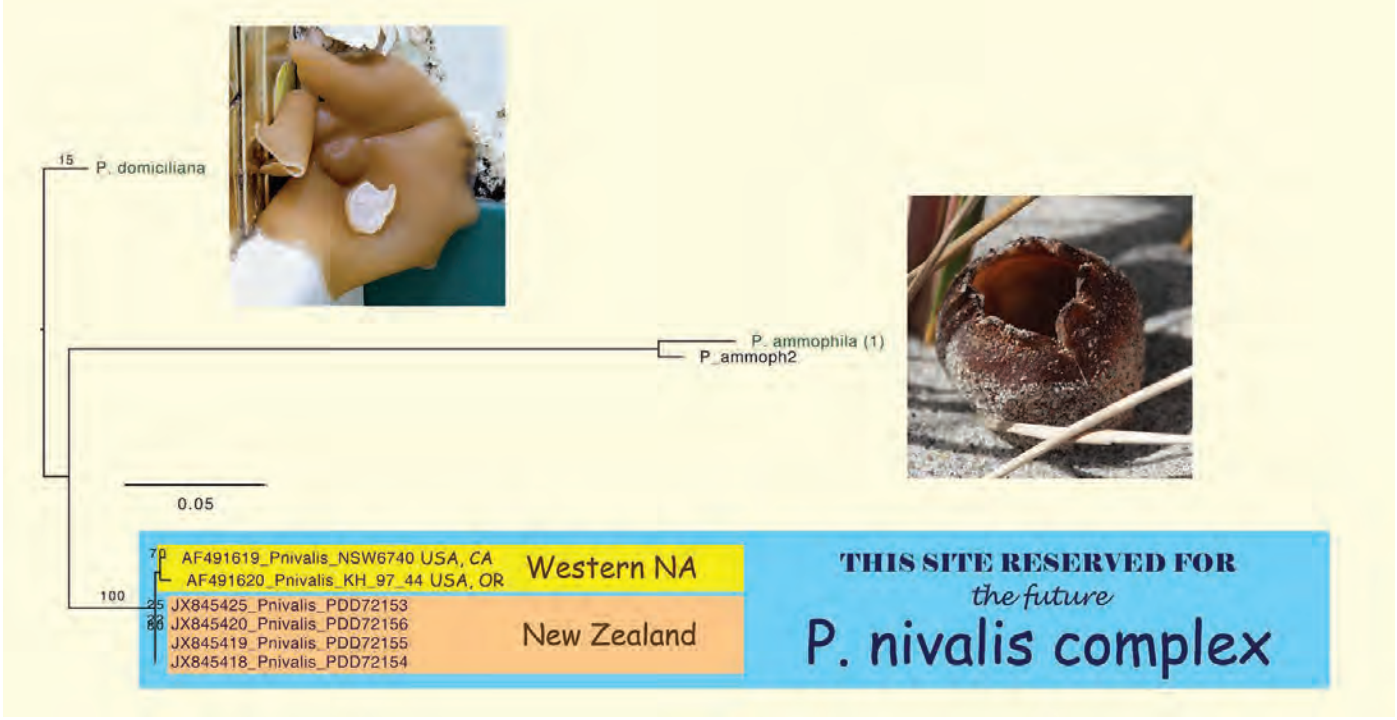

Figure 4: A Maximum Likelihood tree from ITS data of core *Peziza* species, to which some Southern Hemisphere nivaloids have been grafted, and the tree then judiciously pruned, leaving two interesting species we have recorded here, as well as our nivaloid group of interest. The *Peziza domiciliana* shown fruited on a shower stall at our 2009 foray,[17] and *P. ammophila* was collected from the Shallow Bay sand dunes near Gros Morne National Park at our 2014 foray.[18] Both probably represent species complexes. Nivaloid data are limited to collections from mountainous regions in New Zealand and western North America. Both populations cluster in common clade, highly suggestive that they are the same species. The small separation is compatible with geographic variation. Additional collections, representation of other potential species in the complex, and multilocus analysis would be needed to make a definitive statement about conspecificity; sequencing the type (with new typification, if needed) will fix the name and determine the relationship of other populations to *P. nivalis* s. str.

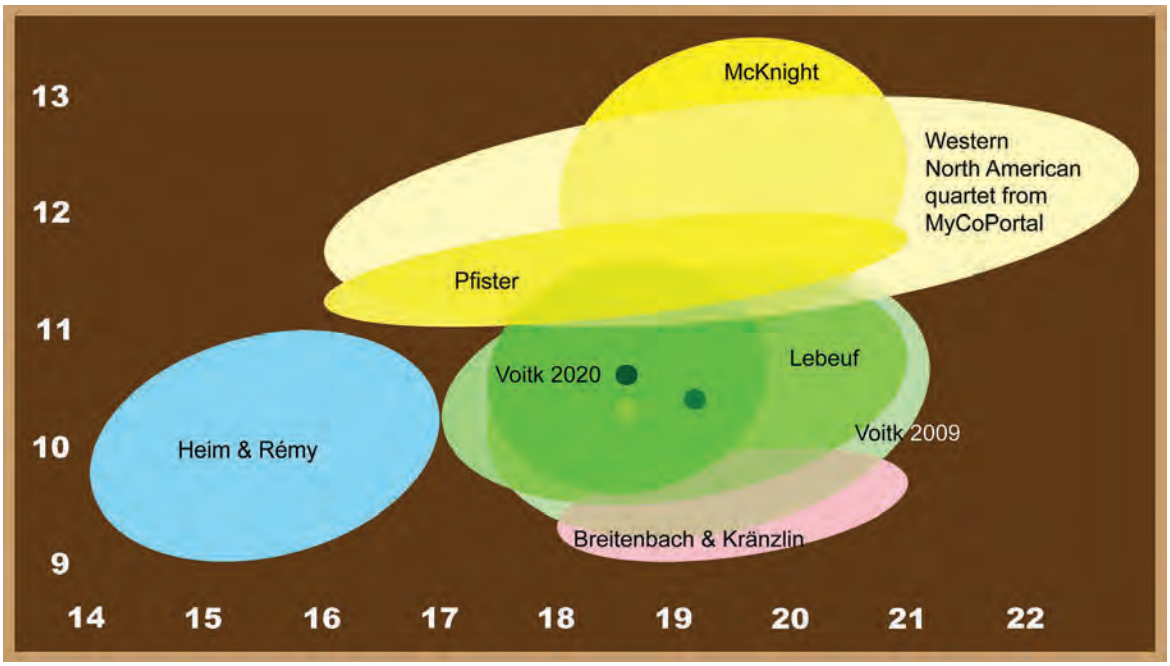

Figure 5: Available spore size data for nivaloid species. Length in µm in x-axis and width on y-axis. Size range in big ovals; where available, average size marked by small circles. Green: *Peziza sp.* "nivenena": all superimposed, suggesting conspecificity. Blue: spore size from protologue of *P. nivalis*. If measurements comparable, this size range is incompatible with conspecificity with *Peziza sp.* "nivenena". Pink: spore size for Swiss specimens as reported in Fungi of Switzerland.[10] Although length fits with *Peziza sp.* "nivenena", the average size (not shown) would be a bit too far from the average size of *Peziza sp.* "nivenena" to be considered conspecific. Yellow: western North American species. Although length may be compatible with *Peziza sp.* "nivenena", the average size (not shown) would be further from the average size of *Peziza sp.* "nivenena" to be considered conspecific.

Figure 6: *Gyromitra leucoxantha* collected May 7, 2020 from other burn site near forest edge, 10 m away from collections of nivaloid discs.

After these speculations, our story is over, and we can go straight to a description of our species. But like all better stories, actually, it is not over. You will recall that Figure 1 showed two burn sites. One yielded the putative *P. nivalis*. The other was the source of four ascocarps of *Gyromitra leucoxantha* (Fig. 6). How cool is that? Both are cool because they fruit at snowmelt time, known as snowbank mushrooms, and nivalis means "from the snow". But this is far cooler than a play on words. *Peziza nivalis* was described from the French Alps, not that far from the Italian border, and *G. leucoxantha* was described from the Italian Alps around Torino, not really that far from the French border.[14] Here, on an uncared-for lawn on the west coast of Newfoundland, in a river valley about 20 m asl are two snowbank species from the European Alps, one from the French side and one from the Italian side, within 10 m of each other. Cool, eh? For a description of *G. leucoxantha* you have to go to a previous issue of Omphalina.[15] There you will learn that the authors sequenced a similar specimen from its alpine type locality (this time on the Austrian side of the Austro-Italian border), which fell in the same clade as the NL specimens, making ours the real *Gyromitra leucoxantha*, and not some similar species in a complex.

Now, go to the description of *Peziza* sp. "nivenena". Because this preliminary review suggests that this may be a different species from *P. nivalis* s. str., for the time being we adopted the code name "nivenena" (**NIV**-alis of – N-[=**EN**]-orth-**E**-astern **N**-orth **A**-merica). The name is a temporary placeholder and not a valid species name; more investigation is required to determine whether this is a different species from the western North American species, and how it is related to other described taxa.

Acknowledgments

We are grateful to collectors and others, who examine collected specimens, record the results and deposit them along with the specimens in public herbaria; we are very grateful that a resource like MyCoPortal exists, whereby information about herbarium specimens is readily available to the public; we are also grateful to have a resource like ASCOfrance available for consultation. We thank Katherine F. LoBuglio for help with the sequence analysis.

Table 1: DAOM accession information for *Peziza nivalis*.

NUMBER	DAOM	NAME	DATE (YYYY.MM.DD)	LOCATION	HABITAT	LATITUDE WGS84, deg.	LONGITUDE WGS84, deg.	ELEVATION (m asl)
09.04.11.av01	DAOM 984760	*Peziza nivalis* complex	2009.04.11	Humber Village, Barry's Lookout	field	48.988302	57.784462	31
20.05.04.av01	DAOM 984761	*Peziza nivalis* complex	2020.05.04	HV 13 Maple	burn site	48.984473	57.768225	11
20.05.09.av01	DAOM 984762	*Peziza nivalis* complex	2020.05.09	HV 13 Maple	burn site	48.984473	57.768225	11

Description

Peziza sp. "nivenena"

Synopsis: Up to 54 mm diameter thin stemless brown disc, somewhat lobular at maturity, with an upper (fertile) surface yellowish brown when young, becoming dark brown to purplish brown and pock-marked with age, appearing on soil, often on burnt ground, in wet areas at snowmelt.

Cup: Diameter up to 54 mm; round with some lobulation at maturity, begins deeply cup-shaped but quickly opens to flat with minimally upturned margins that become somewhat ragged; smooth, in maturity may be pitted with irregularly placed round holes (Fig. 2A) that seem to close when wet (Fig. 2B), and reach the subhymenium (Fig. 2E); occasionally developing minimal radial wrinkling and central puckering with age; hymenial layer first yellowish brown, becoming dark brown with dark purplish tones with age, lighter yellowish brown toward the margin; sterile undersurface finely granular to almost smooth, concolorous with the hymenium or somewhat paler (Fig. 2D). Dries tan-brown to dark grayish brown with minimal purplish overtones. Sporeprint yellowish white (Fig. 7A).

Stipe: absent.

Context: Friable, less than 3 mm thick, weakly layered, darker brown hymenium, light brownish subhymenium; smell unremarkable, taste mild.

Microscopy: [NL specimens: 2020 collection: 10 spores from fresh hymenium of 1 ascocarp; 20 spores from sporeprints from 5 fresh ascocarps (Fig. 7C). No difference noted between the two sources. 2009 specimen: 20 spores from rehydrated dried hymenium of 1 ascocarp. QC specimen: 30 spores from rehydrated ascocarp. All measurements at 1000 × in H_2O mount.] Ascospores 15.4–19.8 × 9.6–13.5 µm, average 18.5 × 10.5; Q = 1.4–2.0, average 1.8. Immature spores have thick, wrinkled walls and granular content, maturing to thin, smooth, walls and hyaline content; asci 280–330 × 15–19 µm, 8-spored, forked croziers at base; paraphyses slender, filiform,

apex subclavate to subcapitate, 6–9 µm wide, septate, often forked at distal septa, 3–5 µm wide, but showing variable fortoulism (Fig. 7B); rehydrated NL specimen showed filiform subclavate paraphyses, most of which failed to inflate.

Habitat (Fig. 1): Open clearings in coastal lowlands.

Substrate: Moist soil with charcoal and woody and herbaceous debris.

Season: Snowmelt in April–May.

Comments: It is interesting to note that spore morphology and size was comparable whether spores were from fresh or dried specimens, and whether they were shed or in the hymenium. In a H_2O mount, the walls of mature spores appeared smooth. Cotton blue has been reported to show microscaly spore wall ornamentation.[16] Electron microscopy of mature cells from the western North American population shows low wrinkling of the cell wall.[11, 13]

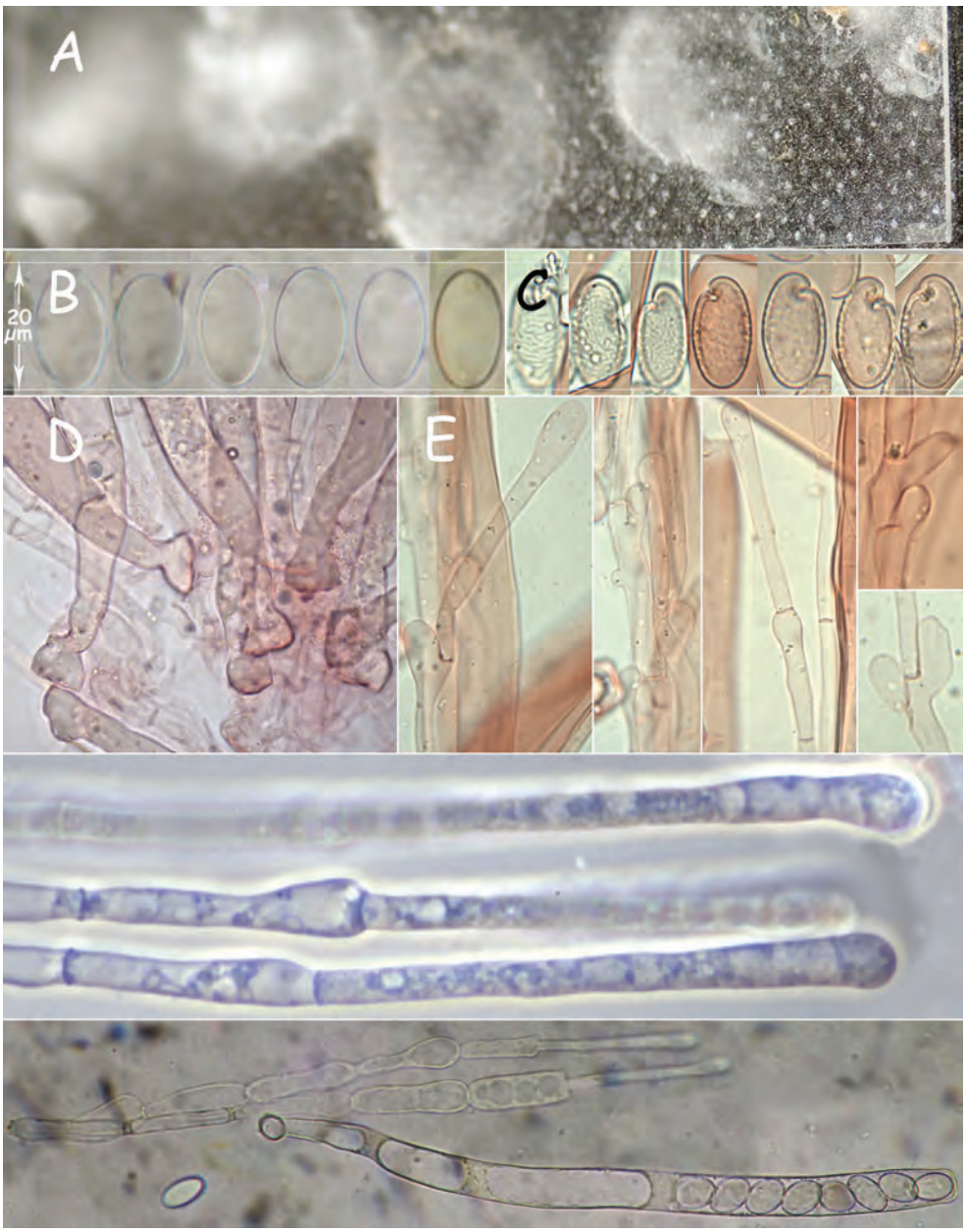

Figure 7: Sporeprint and microscopic findings of *Peziza sp.* "nivenena".

(A) Sporeprint of 2020 NL collection. Difficult to appreciate with certainty here, but colour is subtly to the yellowish side of pure white. Take our word.

(B) Mature spores in water mount under 1000 × (oil) magnification. 20 µm between white lines. Note thin, smooth wall and hyaline content.

(C) Immature spores. Note smaller size, double wall, granular, darker content. Note wrinkling of the outer wall or perisporium.

(D) Bases of the asci, showing croziers that are forked (technical term: pleurorhyncous), quite broadened in this case. Croziers are the ascomycete equivalent of clamp connections in basidiomycetes, have the same function, and have similar value for identification.

(E) Encompasses all remaining images to show variable degree of fortoulism of paraphyses, from minimal swelling to uniform or varied widening, and variable degrees of branching. Variable magnification. An ascus with two fortoulistic paraphyses. Terminal cells remain filiform with a subclavate head.

Peziza nivalis—afterword


Figure 8

A year has passed since the above observations. This was the mildest winter, with the earliest snowmelt in the 22 winters I have spent in NL. The first robins have arrived and a new crop of pezizas presented itself for examination in the same place on our lawn. This time I was waiting for them, so saw them from the first appearance onwards. My collaborators Renée Lebeuf and Don Pfister were right about the development of the species with time. The mushrooms presented as 4–5 mm globes with a tiny upper opening. They opened up as they enlarged, until they became flat with an upturned edge. The young specimens were light and began darkening after flattening. Pockmarks in the hymenium, as suggested by Lebeuf and Pfister, only appeared in the late stages. Microscopically, Donadini's observations were also corroborated: fortoulism was not observed until the mushrooms had aged, darkened and flattened.

As Donadini, Lebeuf and Pfister suggested, the youngest specimens were closest to the receding snow, the oldest the furthest away. This enables one to reconstruct this developmental picture at one sitting. The specimens on Figure 8 were photographed on the same day, arranged sequentially from closest to furthest from the receding snow edge. You can readily see the development of size, shape, and colour, and appreciate the lack of hymenial pockmarks at this stage. Only the largest showed mild fortoulism. As I said, it is easy to write these articles and descriptions if you work with knowledgeable collaborators.

-av

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