OMPHALINA

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Foray Newfoundland and Labrador is an amateur, volunteer-run, community, not-for-profit organization with a mission to organize enjoyable and informative amateur mushroom forays in Newfoundland and Labrador and disseminate the knowledge gained.

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Accepting Contributions

We eagerly invite contributions to Omphalina, dealing with any aspect even remotely related to NL mushrooms. Authors are guaranteed instant fame—fortune to follow. _Issues are freely available to the public on the FNL website.

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Cover image: *Chromosera lilacina*, one of a beautifully coloured genus recently split from *Hygrocybe*. This image was taken during the 2005 Foray in the Labrador Straits by Tracy Keats. For more on how this, and other pretty little *Chromosera spp.* played a leading role in an international story of intrigue, see p. 28.

Message from the Editor

Hello again, friend of fungi!

If, like me, you are terribly disappointed that the Foray this year is not possible due to global health concerns, then I hope Foray NL President Helen Spencer's note (reprinted from her April email; next page) will provide some clarity. It's comforting to know that the organizers are working behind the scenes to ensure that when we can get together again in person, it will be AWESOME. In the meantime, who better to thrive in these times of social distancing than a ragtag group of foragers and mushroom-enthusiasts! We're pros at this. All the more reason for you to stay out of my chanterelle patch anyway, eh?

The days are finally long here on the Avalon, and our first vernal fungi are popping out. I'd say "up", but in the spring the few fungi we do see are always growing up off of something, or out of the side of something else. Never just a simple "up". Many of these first spring finds are ascomycetes, or more commonly, the sac fungi. Now is our chance to really appreciate this understated group, as they are often eclipsed by our flashier mushrooms in the fall. Keep an eye out for a haphazard splash of tiny, electric orange *Byssonectria terrestris* across a wooded path, or a cluster of otherworldly *Peziza* cups on a gravel road looking like the remnants of an abandoned clutch of alien eggs. Or pull out your hand lens and marvel at the elegantly hirsute structures of *Lachnellula agassizii* on conifer bark. The springtime fungi are for the lover of the weird and wonderful. And oh, hey, that's us!

Sara

Byssonectria terrestris

Lachnellula agassizii (and at right)

Foray Matters &

Message from the President

Hello Foray NL Members,

Regretfully the Board of Foray NL have decided to cancel this years Foray at Lion Max Simms Camp. There are a lot of moving parts to organizing a foray and, with so much uncertainty caused by the COVID-19 pandemic, we felt that we would not be able to offer the same value, quality and safety as past Forays.

The good news is that your membership in Foray NL will be extended until the time of the next Foray and you will benefit from notice of early registration at that time and from receiving Omphalina.

In the interim we will be looking at options for offering informative fungal and lichen events online—more on this soon.

Keep an eye on our website, Omphalina, and our social media outlets (Facebook @ForayNL or Instagram @ForayNL) for updates.

There will still be an Annual General Meeting this year, probably in early October, with notification at a later date. The Foray Board is a working board, i.e. we all take on one or more significant tasks. It has a fairly diverse set of skills, but we can certainly benefit from new perspectives, so if you have an interest in joining the Board next fall, please let me know.

Meanwhile I wish you well over the coming months and look forward to seeing you at the next Foray. Have a great mushrooming year.

Best wishes,

Helen Spencer
April 22, 2020

The *Chromosera* of Newfoundland and Labrador

Andrus Voitk, Triina Voitk

Almost two years ago Renée Lebeuf asked me to send some specimens of *Chromosera* to Patrice Tanchaud in France. On the coastal lowlands, near the mouth of the Severin River, about half way between Brittany and the Spanish border (Fig. 1), Patrice had found what he thought was a hitherto unknown species, closely related to *C. lilacina*. Comparing a potentially new species to closely related ones is the best way to learn whether it is really different, and if related, enables circumscription of the new species (defining where the borders are that differentiate it from similar close relatives). We were pleased to send Patrice portions of our collections to help study the new species.

The reader of Omphalina will recall that *Chromosera* is one of the genera derived from the formerly much bigger *Hygrocybe*, when that genus was split into several smaller ones.[1] To get an idea of what we are talking about, think of a pretty, colourful *Hygrocybe*. Or look at

Figure 1: Source of specimens. Green star represents site of Patrice Tanchaud's *C. ambigua*. Red star on North Pole. Lilac circles represent *C. lilacina* collections and yellow ones C. xanthochroa. Overlap prevents showing all collections. In NL they come from Labrador and the Northern peninsula, except for one *C. lilacina*, from the Gros Morne Park area and one from the tundra heath of Signal Hill by St. John's. Note also the two collections, one of each species, from Havøysund, Norway (Fig. 3), almost as far north as you can go in Norway without leaving land. Map adapted from Google Earth.

Figure 2. *Chromosera lilacina*. Photographed in 2005 in the Labrador Straits by Tracy Keats. No voucher kept.

Figure 2. The veteran of our forays will remember the beautiful *C. lilacina* (at the time known as *Hygrocybe lilacina*) collected at our first Labrador foray in 2005. It was first recorded by Noah Siegel and Tracy Keats, and Tracy took the lovely photo. *Chromosera* species differ from those of *Hygrocybe* and similar genera by yellow and lilac colours, dimpled yellow-orange-brown ± lilac caps, decurrent gills, and—for our two species—growth in arctoalpine habitats (title banner, Fig. 3).[2]

The results of Patrice's efforts are now out in print: the species he found was, indeed, new, a sister species to *C. lilacina*, and is described as *Chromosera ambigua* in Persoonia's beautiful Fungal Planet series.[3] Congratulations, and well done, Patrice and collaborators!

Here the story ends for Patrice, and begins for us.

We had always thought that the two species of *Chromosera* in the province were the pretty lilac-orange-yellow *C. lilacina* mentioned, and *C. citrinopallida*, a bright yellow species that turns white on exposure, drying or aging. With one lilac and one yellow species, differentiation should be easy, right? Not entirely, because *C. lilacina* can lose all of its lilac colour with age and exposure, as well as the brownish orange of the caps, to become similarly yellow and even whiten. Usually some remnant of a lilac tint can be found in at least one specimen in a group, so that we interpreted any trace of lilac as a sure sign of *C. lilacina*. Microscopic examination, which can often distinguish species, was unhelpful here, because both species are known to have similar micromorphology with spores of virtually the same size.[4] Therefore, we were confident of our identification and did not examine them microscopically, particularly because the yellow ones fit the description of *C. citrinopallida* so well, and partly because two people familiar with these arctic-alpine species had independently identified our photos as *C. citrinopallida*. In retrospect this seems either too indolent or too hubristic, because molecular studies carried out by Patrice's collaborator, Patricia Jargeat, revealed that our yellow species was not *C. citrinopallida* as we had thought, but *C. xanthochroa* instead.

This makes macroscopic identification more difficult, because in addition to yellow, *C. xanthochroa* also has variable amounts of pale lilac colour (Fig. 4), although more ephemeral than that of *C. lilacina*. Therefore lilac becomes an unreliable character to identify either species. Furthermore, because both may lose their lilac, yellow is also not a dependable differentiating character for either species.

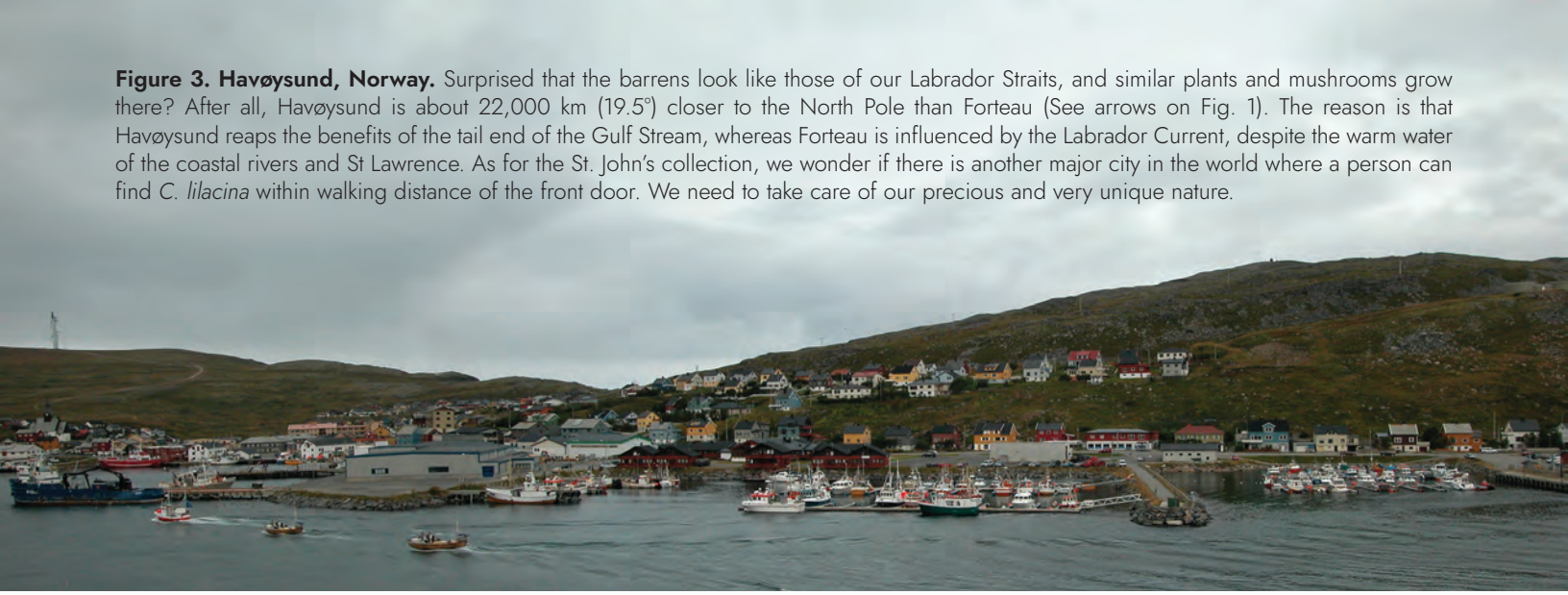

Figure 3. Havøysund, Norway. Surprised that the barrens look like those of our Labrador Straits, and similar plants and mushrooms grow there? After all, Havøysund is about 22,000 km (19.5°) closer to the North Pole than Forteau (See arrows on Fig. 1). The reason is that Havøysund reaps the benefits of the tail end of the Gulf Stream, whereas Forteau is influenced by the Labrador Current, despite the warm water of the coastal rivers and St Lawrence. As for the St. John's collection, we wonder if there is another major city in the world where a person can find *C. lilacina* within walking distance of the front door. We need to take care of our precious and very unique nature.

Fortunately, this time microscopy can be of help, because the spores of *C. xanthochroa* are reported to be shorter than those of *C. lilacina*.[4] Measuring 20 spores should settle the issue in most cases, if you only have these two species to consider.

Ours is a comedy of errors.

1. As just reported above, out of two available yellow *Chromosera* species, we selected the wrong name for our yellow one for want of microscopic examination.

2. Sequencing our collections also showed that we made a classical error, predicted by Boertmann,[4] who wrote that rarely the woodland yellow *Gloioxanthomyces nitidus* may be encountered in tundra habitat, where it becomes a trap for the unwary. As faithful readers of Omphalina, we were familiar with *G. nitidus* from Boertmann's articles in the past,[5,6] and thought we would never be fooled! More hubris. Sequencing showed that we had indeed identified a tundra collection of *G. nitidus* as our yellow *Chromosera* (Fig. 5).

3. The errors do not stop there. Remember how we said that the lilac *C. lilacina* can sometimes turn entirely yellow, and thus be mistaken for a yellow species? You guessed it: we collected one such specimen from atop Signal Hill near St John's and even reported it as *C. citrinopallida*,[7] thus doubling the error in public, because a) our yellow species is not *C. citrinopallida*, but *C. xanthochroa*, and b) this all-yellow mushroom was not our yellow species, but *C. lilacina*, bereft of all its lilac colour to become yellow and white (Fig. 6). This error was all the easier to make, because the lilac colour of *C. xanthochroa* is very seldom seen in NL collections, and then only very subtly (Fig. 2).

Note: the second author did the microscopy on all specimens, but was in no way associated with all the other errors, blunders, mistakes, goofs or other boo-boos described, which must solely rest on the shoulders of her grandfather, the first author, despite his attempts to spread the blame by the use of the first person plural. There was no "we" when the errors were made. *We* came into the picture only when things had to be set aright.

Summary: if there is a mistake that can be made with these species, we made it.

The last-mentioned error was bared after microscopic examination of our collections. Not all had been sequenced, but now that we knew we had two species with different-sized spores, we examined them all. The difference in spore size allowed us to identify the unsequenced collections microscopically with confidence. For your interest, we have plotted these measurements in Figure 7. Spore size is determined genetically, so that when sizes differ, they are as reliable differentiators as molecular studies, but can be done by amateurs without access to the laboratory.

How certain are we that now we have identified all our species of *Chromosera* correctly? Well, first of all we need to collect and sequence more specimens to be certain that we only have two species of the genus. If the current sampling is accurate, the only concern is the correct application of the names to the species clades. This can be ascertained by sequencing the type collections, to make certain that they fall into the same clades. If types are not available or do not yield sufficient amplifiable DNA, new matching collections from the type region need to be sequenced and assigned type status. We have no concern that identifications will change, but

Figure 4. Examples of subtle lilac colour. A. *C. lilacina*, **B–D**. *C. xanthochroa*. **A.** GNP-139, Cape Raven Trail, Great Northern Peninsula, 2012. Brownish-orange tones, rather than yellow suggest the species, as does the remaining lilac in the stem. Identified by spore size. **B.** GNP-110, Burnt Cape, 2012. Whitened cap of one and upper stem of another shows some very subtle lilac. Identified by sequencing and spore size. **C.** SA5-060, Goose Cove, Great Northern Peninsula, 2012. No voucher kept, so identity cannot be confirmed. Violet on stem light, but unmistakable. **D.** 07.08.28.av03, Havøysund, Norway. Suggestion of lilac on gills and upper stem. Identified by sequencing and spore size. Photos A–C: Roger Smith.

Figure 5. *Gloioxanthomyces nitida*. FI2-0306, from tundra-like barrens on Fogo Island, 2013. Dry and white in the exposed area, looking like a yellow Chromosera. Photo: Roger Smith.

Figure 6. *Chromosera lilacina*. Entirely yellow with whitened caps. No brown left on caps, or sign of lilac, unless you can let retrospect talk yourself into the subtlest of lilac hue on the gills. Identified by spore size. Tundra heath atop Signal Hill, 2016. Photo: Maria Voitk.

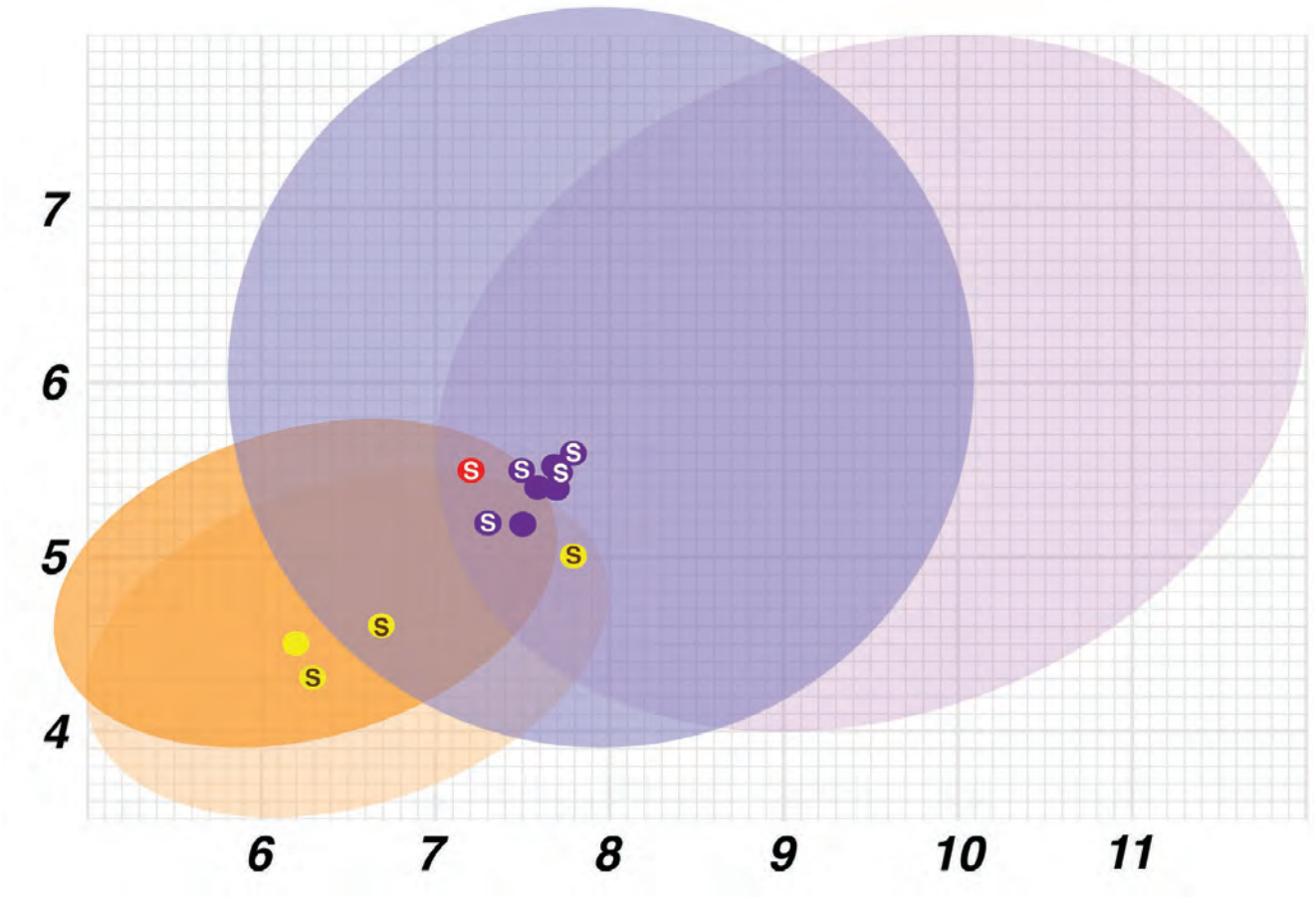

Figure 7. Spore size graph. Measurements in µm, length on the x-axis and width on the y-axis. Range represented by large ovals, lighter ones as reported by Boertmann[4] and darker ones as measured by us. Values for *C. lilacina*, with the longer spores, to the right, and those for *C. xanthochroa*, with the shorter spores, to the left. A single wide *C. lilacina* spore caused the circular shape for our range measurements; otherwise it would have been oval like the others. Normally one would drop outliers, but because we operate with average values, this does not disturb our values significantly. The small dots represent average values for each collection (a minimum of 20 spores each time, from 1–3 basidiomata, by 1–2 observers). S indicates sequence-identified collections. Red represents the collection identified as *Gloioxanthomyces nitidus*, yellow represents *C. xanthochroa*, and lilac *C. lilacina*. The *C. lilacina* specimens cluster together very nicely, as one might expect when working with averages. The *G. nitidus* collection is close by, and, indeed, its spores are reported to be in the same range.

Three collections of *C. xanthochroa* also cluster together, but a fourth collection is far away, and seems to cluster with *C. lilacina*. As you can see, it was identified by molecular studies. Two independent observers checked the spore size from three different basidiomata from the collection, without knowledge of the expectation, and no range varied more than 1 µm from any other, with matching average values. As a result, we are very confident that the results are accurate.

How to explain this seeming discrepancy? One possible explanation is that the spore size for *C. xanthochroa* is much wider than appreciated. The range for spore length for this collection was 5.8–9.6 µm. If this were a legitimate spore range for the species, its range would be double what anybody had ever observed before. Highly unlikely. Similarly, there is no reason to doubt the accuracy of the molecular study.

The most likely explanation is an error in the labeling of the specimen somewhere in the process. In other words, a mismatch between the analyzed specimen and its original collection number. In our experience, when dealing with many samples, such errors are not unusual. These specimens are taken in and out of bags, boxes or sachets several times, as are their tags, and numbers recorded into logbooks. A slip-up at any of these manipulations is possible. When we took our sample from its bag and put a portion in another bag for shipping—along with several other similar samples we sent at the same time—one could have gotten mixed up or repeated or had its tag copied erroneously or switched or… any number of similar mechanical errors could have happened. If it didn't happen here, it could have happened at any of the stages where similar processes are repeated at the laboratory, or results entered in a log. Because the spore size has been checked and double-checked, we suspect a transcription or similar inadvertent error with the recordkeeping as the most likely reason for this discrepancy. We consider the collection to be *C. xanthochroa*, and have treated it that way, despite the reported result, which we suspect originated from a different collection. "Science" is no different from any other human undertaking.

typification with sequenced material is the step whereby names can be fixed and taxonomy stabilized. Now that we are this far, this step cannot be far behind.

Our minor comedy of errors is a very small example of the value of our foray collection. Thanks to a nice collection, we were able to provide specimens to other investigators, which helped circumscribe a new species in France. A valuable side benefit of this was to learn the exact species native to our province. Identifying two species may not sound like a major achievement, but these arctoalpine species are very understudied, particularly in North America: no standard mushroom text includes them. Table 1 presents an updated summary of our collections. Now future identifiers in NL can apply a correct name to their finds with reasonable confidence.

A description of our two species of *Chromosera* follows, based solely on our collections, including the ones from Havøysund, Norway (Fig. 3), which did not differ from ours; descriptions may differ somewhat elsewhere or with a larger sampling.

Acknowledgments

We thank FNL for the opportunity to study these collections, Guillaume Eyssartier for the molecular study results, Tracy Keats, Maria Voitk and Roger Smith for the use of their photographs, and Guillaume Eyssartier and Patrice Tanchaud for sharing the results and valuable suggestions on reviewing the text.

TABLE 1. COLLECTIONS STUDIED

Collecting nr	DAOM*	Date	Final ID	Location	HABITAT	SUBSTRATE	TREES
FI2-306	**981263**	7/Sep/13	*Gloioxanthomyces nitidus*	Fogo Island, Payne's Trail, NL	Heath, barrens	moss/soil	*Juniperus*
07.08.28.av03	**981264**	28/Aug/07	*Chromosera xanthochroa*	Havøysund, Finnmark, NORWAY	Heath, barrens	turf	
BH-103 (BI-33)	**981265**	21/Aug/08	*Chromosera xanthochroa*	Battle Harbour, NL	Heath, barrens		
GNP-110	**981266**	19/Sep/12	*Chromosera xanthochroa*	Burnt Cape, GNP, NL	Heath, barrens		*Empetrum*
GM5-266	**981267**	7/Sep/05	*Chromosera lilacina*	Tracy's Hill, Red Bay, NL	Barrens by coniferous forest	lichen	
07.08.28.av04	**981268**	28/Aug/07	*Chromosera lilacina*	Havøysund, Finnmark, NORWAY	Heath, barrens	turf	
BH-104 (CE22)	**981269**	21/Aug/08	*Chromosera lilacina*	Caribou Island NL	Heath, barrens	moss	
10.11.11.av02	**981270**	11/Nov/10	*Chromosera lilacina*	GMNP Green Gardens, NL	Fen in mixed woods	fen	
11.10.01.av03	**981271**	1/Oct/11	*Chromosera lilacina*	Overfalls Brook trail, Forteau, NL	Heath	sandy soil	*Empetrum, Vacciniae*
11.10.01.av04	**981272**	1/Oct/11	*Chromosera lilacina*	Overfalls Brook trail, Forteau, NL	Heath	sandy soil	*Empetrum, Vacciniae*
GNP-017	**981273**	17/Sep/12	*Chromosera lilacina*	Cape Onion, GNP, NL	Heath, barrens	soil	*Empetrum*
GNP-139	**981274**	20/Sep/12	*Chromosera lilacina*	Cape Raven Trail, GNP, NL	Heath, barrens	soil	*Empetrum*
16.10.23.av03	**981275**	23/Oct/16	*Chromosera lilacina*	Signal Hill, St John's, NL	Heath, barrens	moss, soil	

* These collections have now been deposited in our National Herbarium, DAOM, with these accession codes.

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Chromosera lilacina

Macroscopic. Cap 5–25 mm diameter, dome-shaped, but flattens with depressed centre and smooth margin becomes wavy; viscid in youth becoming dry and matte, often with concentric or irregular cracking of superficial layer; translucent, striate, becoming opaque; brownish orange with variable violet colour, which fades, then becomes yellow and may fade to white. Gills decurrent, more so as cap lifts and straightens; orange-yellow to yellow, with variable violet tones that fade with time. Stem 1–3 × 10–30 mm, straight, cylindrical; most consistent site for persistent violet colour, but will also fade to become yellow, Base often covered with light lilac tomentum. Context lilac through straw to whitish. White sporeprint.

Microscopic. Spores 6.8–10.1 × 3.9–8.2 µm, ave 7.6 × 6.5; Q_{ave} = 1.2, ellipsoid, some with some degree of constricted middle, hyaline. Note that one extra wide spore caused a wide range, and maximal width without it was 6.7 µm. Basidia mostly 4-spored. Cystidia not seen. Clamp connections in all tissues.

Habitat, Substrate, Season, Distribution. Arctic alpine exposed regions, ericaceous tundra heaths, summer to fall. Known circumpolarly from the Nordic countries, European Alps, Alaska and Greenland; in NL known mostly from the Great Northern Peninsula and Labrador, with a single collection from Gros Morne National Park and one from Signal Hill (Fig. 1).

Chromosera xanthochroa

Macroscopic. Cap 5–24 mm diameter, dome-shaped, but flattens with depressed to umbonate centre and margin becomes somewhat wavy; viscid in youth becoming dry, often with some radial cracking of superficial layer; translucent, striate, becoming opaque; bright yellow, becoming white. Very light lilac tone only seen on one cap (Fig. 4). Gills decurrent, more so as cap lifts and straightens; yellow to straw. Very subtle violet maybe seen in one of our three collections (Fig. 4). Stem 1–3 × 10–35 mm, straight, cylindrical; yellow, fading to whitish. Slight lilac tone seen only once (Fig. 4). Context straw to whitish. White sporeprint.

Microscopic. Spores 5.8–7.7 × 3.9–5.8 µm, average 6.4 × 4.5; Q_{ave} = 1.4, ellipsoid, some with some degree of constricted middle, hyaline. Basidia mostly 4-spored. Cystidia not seen. Clamp connections in all tissues.

Habitat, Substrate, Season, Distribution. Arctic alpine exposed regions, ericaceous tundra heaths, summer to fall. Known circumpolarly from the Nordic countries, Great Britain, European Alps, and reported common in Greenland lowlands; in NL known from the Great Northern Peninsula and Labrador (Fig. 1); less common than *C. lilacina*.

COLOR IN MUSHROOMS

Part 1

by Jim Cornish

"Why are some mushrooms so colourful?" I was asked this question by an astute sixth grader during a presentation on fungi back in 2012. After some reflection, I gave what I thought was a reasonable and probably very Darwinian reply: "Maybe it's for the same reason some plants, animals and insects are colourful. It might have something to do with survival." When I later checked my fungi texts and mushroom guidebooks to see if I was at least on the right track, other than recognizing the importance of colouration in mushroom identification, there was no mention of the ecology of mushroom colours. Even the open access scholarly articles available on the Web at that time left the purpose of mushroom colouration largely unexplained.

Since 2012, research on fungal pigments has greatly increased, driven largely by the food industry's interest in fungi as sources of natural food dyes and the pharmaceutical industry's search for new chemicals for the next generation of medications.[1] Yet, some of what has been written about mushroom colour ecology and referenced in this article is largely speculative and not yet tested by vigorous scientific study.

The Ecology of Colour

Colouration in the natural world is remarkably diverse and often visually stunning.[2] Natural colours, including those in fungi (molds, rusts, mushrooms and lichens), are really pigmented secondary metabolites that absorb certain wavelengths of light while reflecting others. Secondary metabolites are considered by-products of cellular metabolism and thousands are produced by plants, fungi, bacteria and algae.[3] Often considered nonessential for growth and metabolic activity, they may relate to defensive and competitive interactions.[4]

Our understanding of the ecology of colour in nature comes mainly from studies of plants and animals[5] who sometimes use colour as a primary defense—a deterrent against direct predator-prey contact.[6] In theory, conspicuous colours, alone or in combination, signal that an organism **may** be secondarily defended, usually by chemical defenses such as toxins, poisons and/or bitter tastes.[7,8] Predators supposedly learn to associate conspicuous colours with noxious side-effects and from a previous experience remember the prey as being unprofitable, i.e. more bother than it's worth. Consequently, "informed" predators tend to avoid novel and conspicuously coloured prey or reduce their attacks over time. Sooner or later, they usually switch to more profitable prey. Young predators who have not yet learned these lessons, either innately know what to avoid or tend to learn via unsuccessful encounters with protected prey. [6,9]

The expression of warning colours is considered a genetic trait[10] that likely arose through the selective pressures of predation.[11] The functional use was first recognized in caterpillars by Sir Alfred Russell Wallace in 1867, used by Charles Darwin in 1874 to support his theory of natural selection and named aposematism by Sir Edward Poulton in 1890.[12] But, what was considered aposematic then has changed over the past 150 years. Seemingly, plants and animals that use colour to advertise their

Figure 1: *Leotia viscosa* is an ascomycete saprotroph formed by hyphal cells embedded in a gelatinous matrix. Does its contrasting blue-green hymenium and yellow stalk make the mushroom appear "novel" and hence protect it from mycophages? Photo: Pieter van Heerden.

Figure 2: *Mycena* species. The white mass at the base and covering the leaf litter is the mycelium, the vegetative body of a fungus. Photo: Pieter van Heerden.

toxicity do not have to be completely avoided to be considered aposematic.[13]

Despite the diversity of colours in nature, those considered "warning colours" are limited to red, yellow, orange and violet hues; the ones identified by ecologists as the most conspicuous against the green and brown backgrounds of nature when seen in daylight and the colours that provide the greatest contrast when seen at night.[2,14] These colours are quite common in mushrooms.

Mushroom Colours

Filamentous fungi produce an extraordinary range of pigments in general chemical classes such as carotenoids, melanins, phenazines, quinones, flavonoids and more specifically pigments such as monascins, violacein, or indigo.[15,16] It has been suggested that colours (and toxins) could be biochemical accidents caused by absorption of an arsenal of chemicals found in the organic material they recycle. It has also been suggested that the presence, or absence, of colour and toxins have resulted from traits gained and lost over evolutionary time. Or, some colours may have simply developed independently as a result of divergence.[5]

Pigments are often synthesized from colourless precursor secondary metabolites that are stored in the fungi's mycelia and combined in mushrooms just before they break through their substrates.[17] Since maintaining pigmentation is an expensive use of resources,[5] mycelia are mostly hyaline (translucent) and *en masse* appear colourless. (Fig. 2) Mycelia can, however, appear yellowish with age and when producing chemical defenses against soil mycophages such as invertebrates and microbes.[18]

Depending on the species, mushroom colours may be confined to the cap cuticle, leaving the stem and flesh either white, creamy, slightly tinted or even a completely different colour. Pigments may also be uniform throughout the mushroom, making all parts similarly coloured. (Fig 3) In some cases, more than one pigment can combine to give mushrooms multiple colours (Fig 4) Pigment colour, saturation, and luminance (brightness) may be influenced by environmental factors such as pH, substrate, oxygen, temperature and water and light availability,[19] so intraspecific differences in colour are common. Mushroom colouration can also vary with age

Figure 3: Carotenoids have been isolated from the yellow, orange and red colours in many ***Cantharellus*** species.[21] In ***Cantharellus roseocanus***, yellow carotenoids are found in the caps, gills and stem. Photo: Pieter van Heerden.

Figure 4: *Suillus clintonianus*. The cap of this larch bolete contains at least 11 yellow, orange and red pigments derived from decarboxylated pulvinic acids.[18] Photo: Andrus Voitk.

Figure 5: *Amanita muscaria var guessowii* showing colours likely due to habitat and environmental conditions. The image was taken on an open grassy strip beside a street. Might the lighter colour in the larger mushrooms be due to bleaching by the sun? Photo: Jim Cornish.

Figure 6: *Cortinarius* species showing variable cap colour due to pigment leaching by rain water. Photo: Pieter van Heerden.

Figure 7: *Cortinarius semisanguineus*. The reddish-brown colouration in this mushroom, and in some *Suillus* boletes, is a result of the concentration of iron.[18] Photo: Jim Cornish.

and when mushrooms are collected, bruised, bleached by sunlight (Fig. 5) or leached by rainwater.[20] (Fig 6) Elements such as iron can also contribute to mushroom coloration. (Fig 7)

Mushroom colouration can also vary depending on the fungi's lifestyle and average and seasonal temperature conditions in their habitats. A 2019 study of over 3054 mushroom images taken in Europe showed that ectomycorrhizal species were on average darker than saprotrophic ones, a difference attributed to ectomycorrhizal mushrooms' abilities to easily obtain a steady supply of carbon via their mutualistic plant partners. The same study also found that dark coloured mushroom assemblages were often more prevalent in colder areas. Additionally, saprotrophic mushrooms were found to be darker during the colder seasons (spring, fall and winter) but lighter in summer. Ectomycorrhizal assemblages, on the other hand, remained darker throughout the year.[5]

Aposematism in Mushrooms?

In terrestrial ecosystems, mushrooms are an important source of food for both vertebrates and invertebrates.[22] Because mushrooms live in close association with many

Figure 8: *Amanita bisporigera*. This nondescript mushroom is deadly, yet it does not advertise its toxicity via any aposematic colours. Photo: Andrus Voitk.

other forms of life, might some varieties use their warning colouration to advertise their secondary defenses against mycophagy?[23] A 2005 study of over 500 guidebook descriptions of mushrooms in North America and Europe concluded that while some poisonous mushroom appear conspicuous, "contrary to expectations and despite a range of analytical methods, there is no evidence that poisonous mushrooms, as a whole, **consistently** signal their unprofitability via colourful visual traits"[24] (e.g. Fig. 8). Why, might be explained by fungal secondary metabolite distribution being based on ecological traits rather than species relationships and lineage.[4]

But, this 2005 study did single out one species as being aposematic: the well-known, and well-studied, *Amanita muscaria*. (Fig. 9) There are credible observations of vertebrates such as birds, opossums, reindeer, wolves, foxes, caribou and deer avoiding these red capped mushrooms. This suggests that these animals may have innately made a connection between the mushroom's conspicuous colouration and its toxicity.[23] It has been suggested that these animals can also weigh the nutritional benefits of eating colourful toxic prey against the potential costs, which might explain why they sometimes eat mushrooms normally avoided.[24] Based on observations of reindeer, it has even been suggested that some animals deliberately seek out and consume colourful psychoactive mushrooms for their psychological effects.[25]

Invertebrates, such as slugs and insect larvae, on the other hand, seem to be unaffected by toxic mushrooms of any colour, maybe because they lack the organs that toxins often target. While not immune from the effects of toxins, small vertebrates like squirrels, chipmunks and hares seem to better tolerate them or maybe their grazing habits reduce the toxin's full effects.[25] Since grazing by all of these small creatures can be slow and/or sometimes limited, the mushroom likely has plenty of time to develop and discharge the bulk of its spores. Under the modern definition of aposematism, limited grazing on conspicuously coloured prey, does not exclude it from being considered aposematic.

Figure 9: *Amanita muscaria* is common to central and western North America. Its variant, ***A. muscaria var guessowii***, (Fig 5) is commonly found in eastern North America, including Newfoundland. Is it also aposematic? Photo: Renée Lebeuf.

Figure 10: *Laccaria* species. Slugs seem to prefer some ***Amanitas, Cortinarius, Russula, Suillus*** and ***Lactarius*** and other varieties but show no interest in ***Laccaria***. Have slugs and some mushroom species coevolved to allow mycophagy while other mushrooms possess antifeedants to deter mycophagy?[26]

Figure 11: *Russula emetica*. In a cluster of these ***Russulas***, it is not unusual to find signs of sampling on only some mushrooms. Photo: Jim Cornish

Figure 12:
Protostropharia alcis.
Spores that germinated inside the digestive tract of moose growing on moose feces.
Photo: Andrus Voitk.

Some conspicuously coloured fungi are secondarily defended by bitter tastes- the mushroom *Russula emetica* being a familiar example. Feeding marks on this mushroom might be evidence not of consumption, but of "sample-and-reject behaviour", a common occurrence on aposematic plants, and a behaviour accommodated within a modern definition of aposematism. (Fig. 10) Sampling allows a grazer to take a bite, to discover something unpalatable, and then to move on without having caused harm to itself or the prey. In my experience, it is not unusual to find within a cluster or troop of *R. emetica* one or two specimens sporting feeding marks, but the remaining mushrooms left untouched. Observations like these also fit within another notion in aposematism; safety in numbers. Gregarious and aposematic plants and animals, and presumably mushrooms, might be kept safe from predation when a sampling of one individual leads to avoidance of the rest in the group.[24]

While brighter colours during the spore developmental stage can warn mycophages and keep some of them at bay,

Figure 13: ***Gymnosporangium clavipes*.** Bright orange aecia (cup clusters) parasitizing service berries (***Amelanchier*** species) mimic flower structures and likely attract insect vectors.[30] Photo: Jim Cornish.

some mycophages might be attracted by these same colours; hence the paradox of aposematism. It has been suggested that some mushrooms may use colour to deliberately attract mycophages as a means spore dispersal. Dark spores that are thick-skinned and protected by melanin, for example, can survive the digestive tracts of animals and arthropods alike. When excreted in feces, the spores have a ready supply of organic matter in which to germinate and grow.[27] Other spores, like those of *Protostropharia alcis*, are known to germinate while in the intestinal tract and have a starting chance when excreted. (Fig. 12)

Figure 14. *Pucciniastum vaccinii,* a bright yellowish leaf rust fungus growing on ***Rhododendron canadense*** (rhodora) might also attract insect vectors.

Colouration Related to Adaptative Resemblance

Around the same time Wallace was promoting aposematism, Henry Walter Bates was exploring mimicry, an adaptive resemblance mechanism displayed by some insect and animal taxa. Mimicry occurs when undefended species mimic the colour signals of defended species.[6] Hence, mimicry fools predators into associating the mimic's conspicuousness with risk, without the mimic incurring the expenses of maintaining a secondary defense.[13] Another adaptative mechanism is crypsis (better known as camouflage) and is the opposite of aposematism. Cryptic organisms hide by resembling random samples of colours from their habitat's background. Crypsis enables sessile prey to avoid detection by predators and mobile predators to avoid detection while stalking their prey.[8]

Although it is often difficult to distinguish mushrooms in a layer of recent leaf litter, especially when viewed at a distance, there is no definitive evidence that fungi are cryptic. There are, however, examples of fungi benefiting by forcing mimicry in some plants.[28] Most common in plant-parasites, this mimicry is aggressive, not defensive in nature. Parasitic fungi often induce its host plant to produce visual and olfactory signals such as brightly coloured pseudo-flowers, false plant-like structures and sweet-smelling scents. (Fig.13, 14) These deceptive adaptations might attract insect pollinators who then vector fungal gametes or infectious spores to healthy plants.[29]

Why are some mushrooms so colourful? The short answer is that we really don't know for sure! Their short life span and the fact that most mushroom varieties cannot be grown under controlled laboratory conditions make ecological studies challenging, if not impossible, to conduct. This gives citizen scientists, like yourself, opportunities to contribute to the discussion by observing interactions between invertebrates and vertebrates in the mushrooms you seek or serendipitously find.

While an aposematic role for mushroom colouration has only limited support in the scientific literature, the importance of pigments in the protection of fungi from environmental stresses other than those posed by mycophages is better documented and is the subject of part two of this two-part series on colour in mushrooms.

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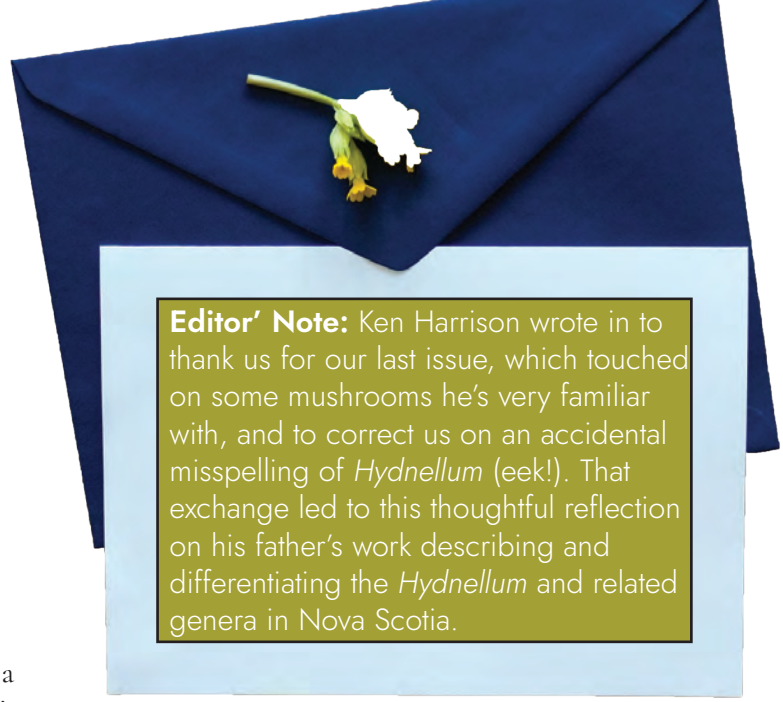
The Bishop's Sketchbook

Artwork by
Glynn Bishop

Background image: Ashley Edwards on Unsplash

THE MAIL BAG



Editor' Note: Ken Harrison wrote in to thank us for our last issue, which touched on some mushrooms he's very familiar with, and to correct us on an accidental misspelling of *Hydnellum* (eek!). That exchange led to this thoughtful reflection on his father's work describing and differentiating the *Hydnellum* and related genera in Nova Scotia.

"My compliments to Andrus Voitk for his response to the "Ask an Expert" item in Omphalina's recent issue. The discussion of *Hydnellum diabolus* and *Hydnellum peckii* with the additional photos shows that distinguishing *H. peckii* and *H. diabolus* will be a challenge for anyone trying to identify these fungi in the field or the lab.

My late father, Kenneth A. Harrison (1901–1991)[1], wrestled with many "hydnums". Dad worked intensively on the hydnums in Nova Scotia and across North America throughout his life, focusing on what are now species in the genera *Hydnum*, *Hydnellum*, and *Sarcodon*. This persisted long after his retirement, in which he collaborated with researchers across North America to continue pursuing his passion for these mushrooms and producing valuable work.

In 1970, he examined the specimens of Drs. H.J. Banker (1866–1940) and W.C. Coker (1872–1953) in the University of North Carolina herbarium at Chapel Hill, North Carolina. The Chapel Hill and the University of Michigan herbaria are the "mother lodes" for the original specimens of many North American hydnums. Last year I came across a nondescript brown envelope that contained about 45 pages of Dad's notes on the ~500 specimens of hydnums held at Chapel Hill. Fortunately, my late mother had transcribed Dad's "hen-scratch" scribble into something very legible back in 1970. Those notes were recognized as valuable by the mycologists at Chapel Hill (they did not have copies). They are now in Chapel Hill and will be associated with the herbarium specimens and copies will be deposited in the University of North Carolina's archives. I am working to sort out a large number of both black & white and their associated Kodachrome colour slides; these will eventually be archived with the material at Acadia University or the University of Michigan, or possibly in Ottawa. I am guessing that he left somewhere between 5,000 and 10,000 colour slides that need to be sorted. This will be a long-term project. Every attempt to tidy up and sort material becomes a voyage of discovery!

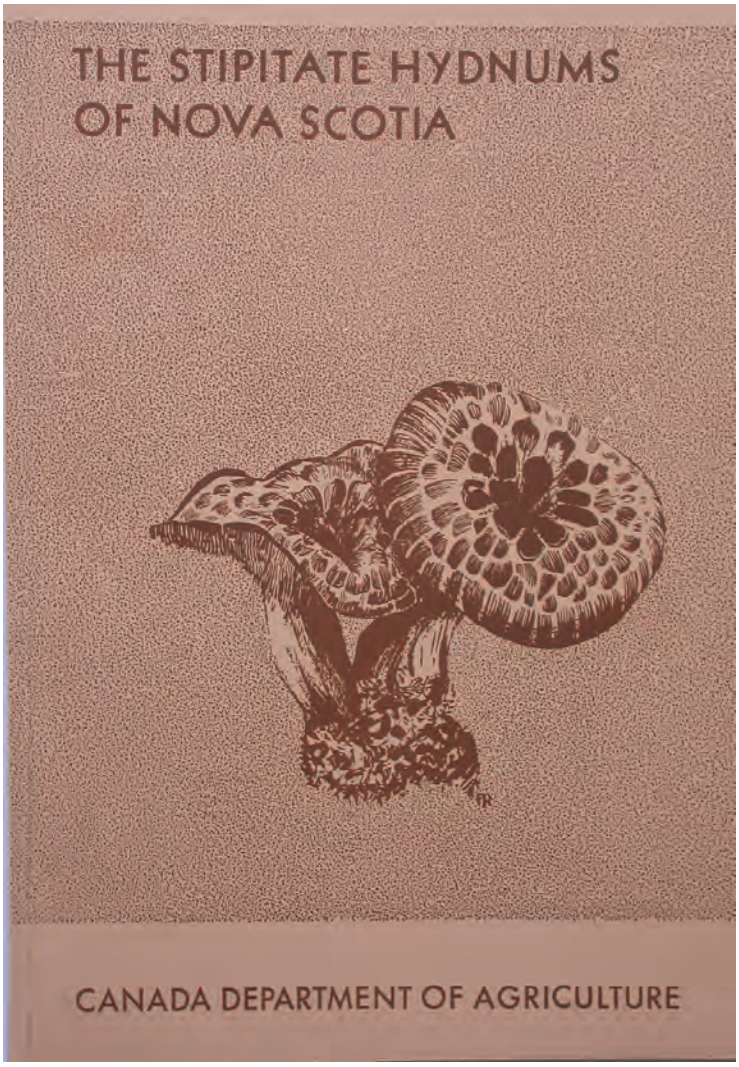
By the mid-1950's he had become friends with Dr. Alex Smith, a prodigious mycologist at the University of Michigan in Ann Arbor, Michigan. Alex was the author of the first popular mushroom field guide, The Mushroom Hunters Field Guide, published in 1958. It was originally illustrated with black and white pictures that were quickly replaced with excellent colour pictures as it went through many successful editions. The guide set the standard for all subsequent field guides. He and his daughter, Nancy Smith Weber, revised The Mushroom Hunter's Field Guide and together they produced regional field guides to western and southern mushrooms. Many of Alex's published monographs are the starting point for serious investigations. The names may have changed, but his work remains.

After his retirement in 1966, my Dad spent about five of the next seven years associated with Alex at the University of Michigan. Alex had a large number of talented Ph.D. students who went on to teach and collect throughout the USA. Dad shared lab space with a number of Alex's students in the late 1960's and many of their own future students in later years.

Dad's return to Canada in the early 1970's renewed his long association with nearby Acadia University and Dr. Darryl Grund, a mycology professor in the Biology Department. Over about 15 years, Dad worked with

Darryl's honours and graduate students at Acadia during the collecting seasons and into the academic year, before heading back to the University of Michigan from January until March to work on his hydnum collections. Retirement, indeed!

If you are interested in exploring the difficult world of the hydnums, you can expect many challenges. There are few useful microscopic characters useful to distinguishing between species, and they have odd, irregularly bumpy spores that are similar in size and difficult to measure accurately. The fruiting bodies are incredibly variable in form and colour, and react to wet or dry weather in odd ways. *Hydnellum* spp. extrude brightly coloured droplets during rapid growth in wet weather. These droplets can dry up and stain the tops during hot weather or when bleached by the sun. Those same fruiting bodies are long-lived and can renew growth after a drought and produce a wide variety of forms.



Where to begin? I suggest The Stipitate Hydnums of Nova Scotia[3] published by the Canada Department of Agriculture in 1961 that has 30 colour photos and is available in various digital forms online. You can follow that with a subsequent Canadian Journal of Botany article[2] that is also available online.

After many years of North American collecting Dad seems to have settled firmly on *H. diabolus* as the "hot" one. Sadly, he never had the resources to explore and collect in Newfoundland and Labrador.

I welcome the rise of DNA nuclear analysis to sort out these conundrums. It will take time. As long as the researchers preserve voucher material and take good photos, I am on board! BUT... I make no claim to be up-to-date on what was once called the "Hydnaceae".

Ken Harrison
Kentville, NS

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The Empty Skillet

Baked Mushroom and Tuna Gnocchi

I admit I was skeptical about this one, but the combinations of flavours is rich, earthy, and utterly outstanding. Make sure you use high quality tuna packed in olive oil. Any mushrooms will do; all the better with last year's preserved or frozen harvest. I like the combination of oyster and lion's mane for their contrasting textures.

Ingredients:

- Package shelf-stable or fresh potato gnocchi; cooked according to package and set aside
- 4 cups mixed mushrooms (chop fresh and reserve preserved/frozen)
- 2-4 cloves garlic (to your taste)
- 1 tbsp. olive oil
- 250 mL heavy cream
- 1 can tuna, packed in oil
- Parmesan cheese, grated or shaved

Directions:

Preheat oven to 425°F. Butter a large casserole dish and set aside. Cook raw mushrooms on medium high heat until they dewater; lower heat to medium and add garlic and olive oil to pan for last few minutes. Add any reserved mushrooms. Add cream and simmer to thicken slightly. Fold in cooked gnocchi, tuna and grated parmesan. Transfer to buttered dish and top with herbs (I like to add finely chopped black kale and Barking Kettle's alder pepper on top). Bake for 15 minutes. Enjoy!

Recipe from Sara Jenkins; adapted from Better Homes and Gardens 2013.

ASK AN EXPERT

Our home's primary heat source is a wood stove. Every year we burn about 4 cords of birch which we buy as 8 ' lengths and then cut and split in July. We then stack the wood to let it dry ready for burning between 6 months and 20 months later. This year, for the first time, I'm horrified to see that instead of drying nicely, much of our firewood is rotting. Instead of the cut ends turning a lovely golden brown, some of is it is turning black, some of it has a pinkish white smooth growth and some of it is beautifully frilly with small bracket fungus developing. See the photos. Besides it being a particularly wet fall, is something else going on to cause this problem?

- HELEN

"THE ISSUE IS THE SAP RUNNING IN THE WOOD WHEN IT WAS CUT.

This acts like an inoculation food source (sap on cut locations) for the many spring sporing mushrooms like small bracket fungus (e.g. turkeytail LOVES sappy birch), and various molds (black ooze).

Birch should not be cut when running sap hard in the spring. Period. Mid-summer, and mid-winter are far better harvest times because the trees are dry and not running sap. The worst is a nice warm late March or April day (when some harvesters LOVE cutting wood). The spring air is cool, with no flies and the days are long, but the wood molds and rots fast thanks to the sugary sap in every cut and the moldy spore filled spring air... especially the cut wood drops as sappy lengths into a pile of leaves on the forest floor.

- BILL BRYDEN

Photo by Radek Grzybowski on Unsplash

Free advice from our expert advisors. Have a question about a fungus in your life? Send it to the Editor at omphalina.ed@gmail.com. *But remember... you get what you pay for!*

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