Pseudoomphalina and Pseudolaccaria of NL

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As a member of a mushroom club with a former *Omphalina* (current *Arrhenia*) as its logo and a newsletter named Omphalina, it behooves you to keep up with the latest about omphalinas and their allies in your neighbourhood, including, of course, the wannabe or pseudo omphalinas. To help you meet that obligation, we published a study of the *Pseudoomphalina kalchbrenneri* complex in North America in the recent issue of Botany.[1]

It began when John Tuach invited the lead author (AV) and his wife to look for mushrooms on his property in Pynn's Brook, near Deer Lake, NL. They finished the day with a stroll along the shore of Deer Lake, where, in the gravel of the beach near some dead alder branches, AV noticed a single small tan mushroom. It was *Omphalina*-like, but not something he recognized (see illustration with description). The specimen was sent to Irja Saar for sequencing, and the DNA came back as a close match for *Pseudoomphalina kalchbrenneri*. AV had never heard of *Pseudoomphalina*, but thought the name must be real, because nobody's sense of humour could be lame enough to make up such a name as a joke. About this time Renée Lebeuf found a nice collection of *Pseudoomphalina pachyphylla* in a sand dune on the road to Terra Nova (illustrated with description). That name has since been changed to *Pseudolaccaria pachyphylla*, but at the time, all of a sudden, we had two species of a genus we did not know existed.

This presented an opportunity to learn about them. *Pseudoomphalina kalchbrenneri* had been known in Europe since its description by Bresadola in 1883.[2] A major review was published in 1995 from the former Czechoslovakia,[3] which included spore measurements of Bresadola's type specimen, and the species was epitypified and sequenced in 2015.[4] The spores of our NL "*Pso. kalchbrenneri*" overlapped the European species on one end, but were noticeably smaller on the other (Fig. 1). Could ours be a different species, even though it looked like *Pseudoomphalina kalchbrenneri*? Might there be other species of *Pseudoomphalina* in North America? Indeed, three other species had been described from eastern North America: *Pseudoomphalina compressipes* by Peck, *Pseudoomphalina felleus* by Kauffman, and

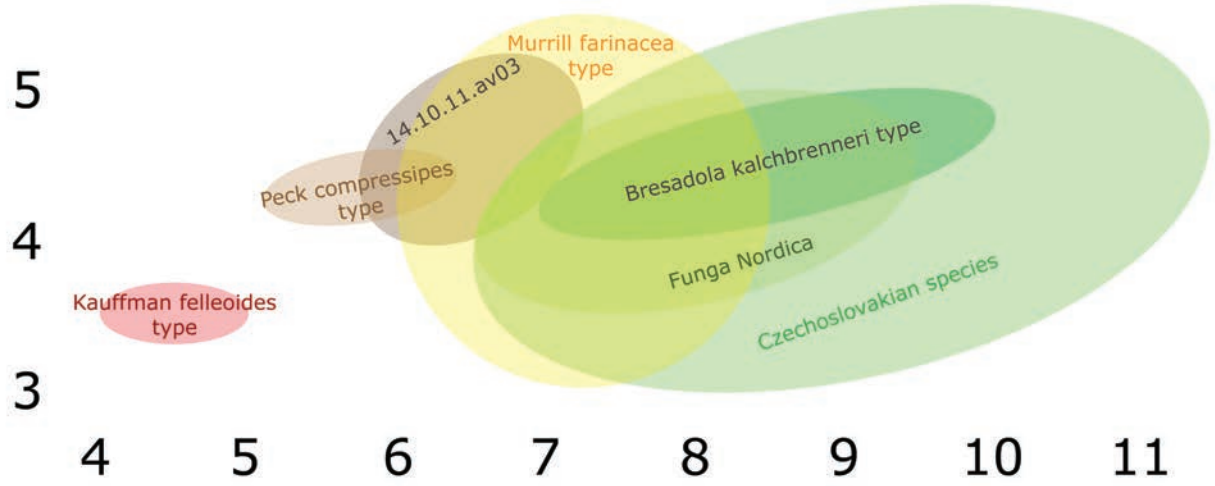

Figure 1: Chart of spore sizes of *Pso. kalchbrenneri* (green) from two European sources and measurements of type specimen by Kotlaba and Pouzar, compared to the Deer Lake specimen (14.10.11.av03) and three described North American species (size as reported by author in protologue). Measurements in µm, length on x axis and width on y. Note that despite marked overlap for most, spore size of all North American species extends lower than that of *Pso. kalchbrenneri*. All three eastern North American species turned out to be conspecific, and are now known by the oldest epithet, *Pso. compressipes*. The spores of Kauffman's species seem considerably smaller than the others. Our measurements confirmed that it did, indeed have smaller spores, but within the range we found for several specimens.

Pseudoomphalina farinacea by Murrill. All had smaller spores than the European *Pseudoomphalina kalchbrenneri* (Fig. 1).

To determine the species native to Newfoundland, Irja Saar sequenced the type specimens for these species. **Surprise**: all three were the same species, and the same as our Deer Lake mushroom, a species different from the European *Pseudoomphalina kalchbrenneri* (Fig. 2). The oldest name for this clade was *Pseudoomphalina compressipes*, so that becomes the correct name for them all, including our Deer Lake specimen.

We submitted these findings for publication, and the reviewers suggested we get a more complete overview of the complex across North America. Perusal of the available collections across North America confirmed that the reason we had found only one specimen in 16 years of collecting was because these are not common species. A quick estimate of the collections available suggested that studying less than 10 additional collections across the continent should produce as complete a picture for North America as is possible at this time.

This additional work proved very fruitful. It confirmed that *Pseudolaccaria* was a distinct genus from *Pseudoomphalina*, and *Pseudolaccaria pachyphylla* was a single species across the Northern Hemisphere, including both eastern and western North America. In contrast, the *Pseudoomphalina kalchbrenneri* complex has diversified into different species. Although the three species described originally from eastern North America turned out to be the same, we found two additional species to make, again, three different *Pseudoomphalina* species across North America (Fig. 2). On the Pacific coast, *Clitocybe intermedia* had to be transferred to *Pseudoomphalina* as *Pso. intermedia*, and in addition to our *Pso. compressipes* (illustrated with description) on the east coast of North America, we also identified a new species, *Pso. anticostica* (illustrated with description), first collected by Renée Lebeuf on Anticosti Island, QC. Although we have only found the former in NL so far, these species occupy the same range elsewhere. Because they are so uncommon, it is likely that *Pso. anticostica* will be discovered here as well, but it may take some time. Or maybe they are more common than we realize, but because they do not stand out, they may have been misidentified as a species of *CIitocybe* or discarded as unidentified specimens at forays.

Identification is difficult because all four species look alike. However, provided you know whether you are in Europe or the Pacific coast of North America, you can ascertain whether you have *Pso. kalchbrenneri* or *Pso. intermedia*, respectively (Fig. 3). The problem comes for us on the east coast, because it seems that both *Pso. anticostica* and *Pso. compressipes* occupy similar habitat

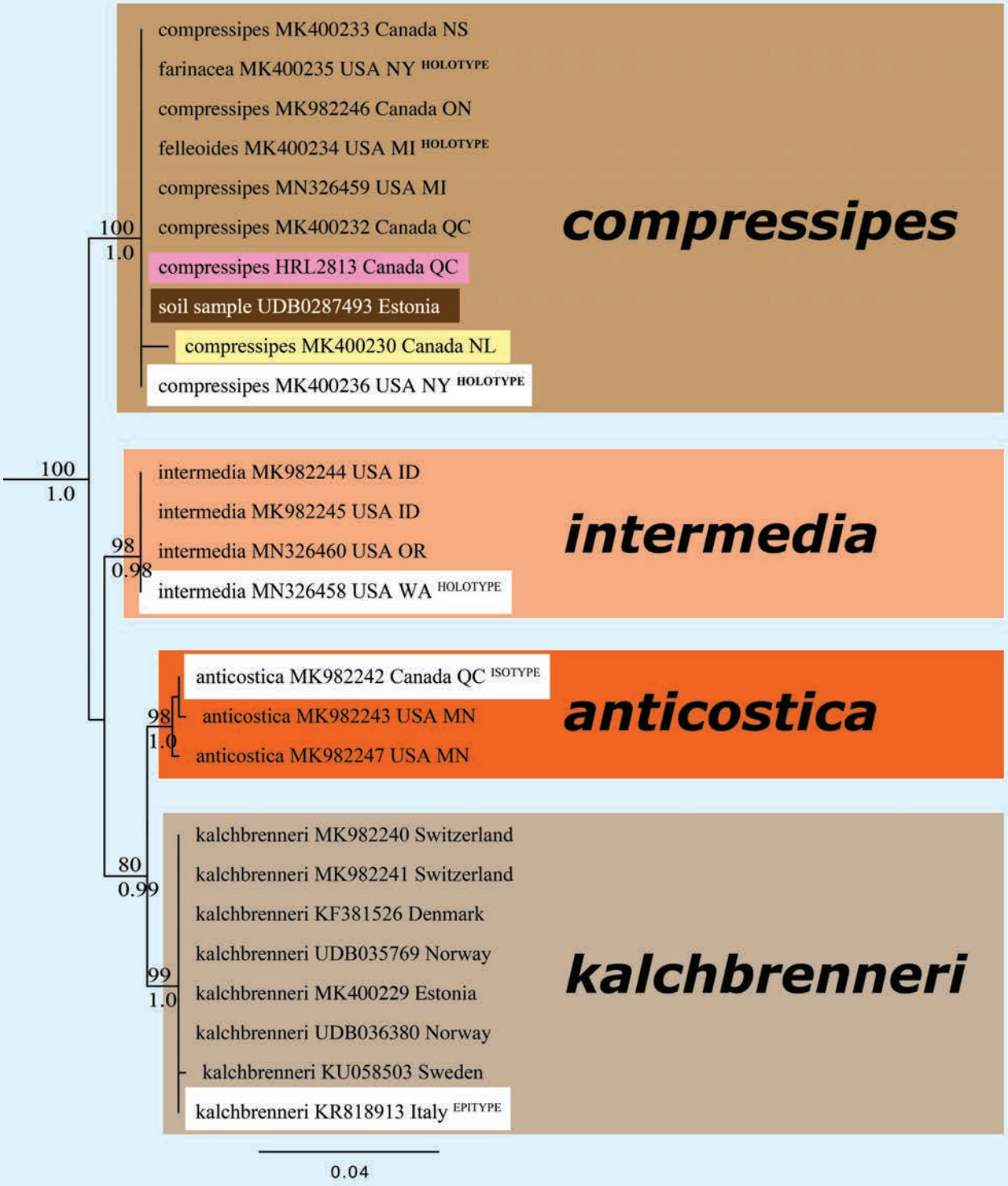

Figure 2: Phylogeny of the known species in the *Pso. kalchbrenneri* complex. The type specimens for each taxon are on a white background, fixing each name. After our first study, we were aware of only the top and bottom species. Because the reviewers asked us to study more, sequencing an additional seven (7!) collections revealed two more species in North America. From above downwards, *Pso. compressipes* from eastern North America; the Deer Lake specimen on yellow background. Note first, that the types for the later-described species *felleoides* and *farinacea* fall in the same clade with *compressipes* (i.e. are the same species). Note also the two additions since our article in Botany: the long-spored specimen from Québec on pink background that caused one of the authors (AV) to lose a Toonie bet to another (RL)—bet hitherto unpaid—and the environmental sample from Estonia on brown background, the first known report that this species extends beyond North America, although a second species of the complex has not been reported in Europe to date. Then *Pso. intermedia* on the Pacific coast of North America, *Pso. anticostica*, the new species, in eastern North America and the European species, *Pso. kalchbrenneri*. Note that *Pso. kalchbrenneri* and *Pso. anticostica* are sister species and also have the longest spores, whereas the more ancestral species, *Pso. compressipes* and *Pso. intermedia* have shorter spores.

Figure 3: World distribution of the *Pso. kalchbrenneri* complex. Knowing whether you are in Eurasia or the Pacific coast of North America will make identification of *Pso. kalchbrenneri* and *Pso. intermedia* easy. However, separation of *Pso. compressipes* and *Pso. anticostica* in eastern North America is more difficult. Spore size, despite significant overlap, may help. At least, this was the case until the DNA of *Pso. compressipes* was found in Estonia. Now we may find that species in Europe as well, changing this equation. Our problem in NL will remain the same: how to tell whether we have *Pso. compressipes* or *Pso. anticostica*, provided the latter is shown to grow here.

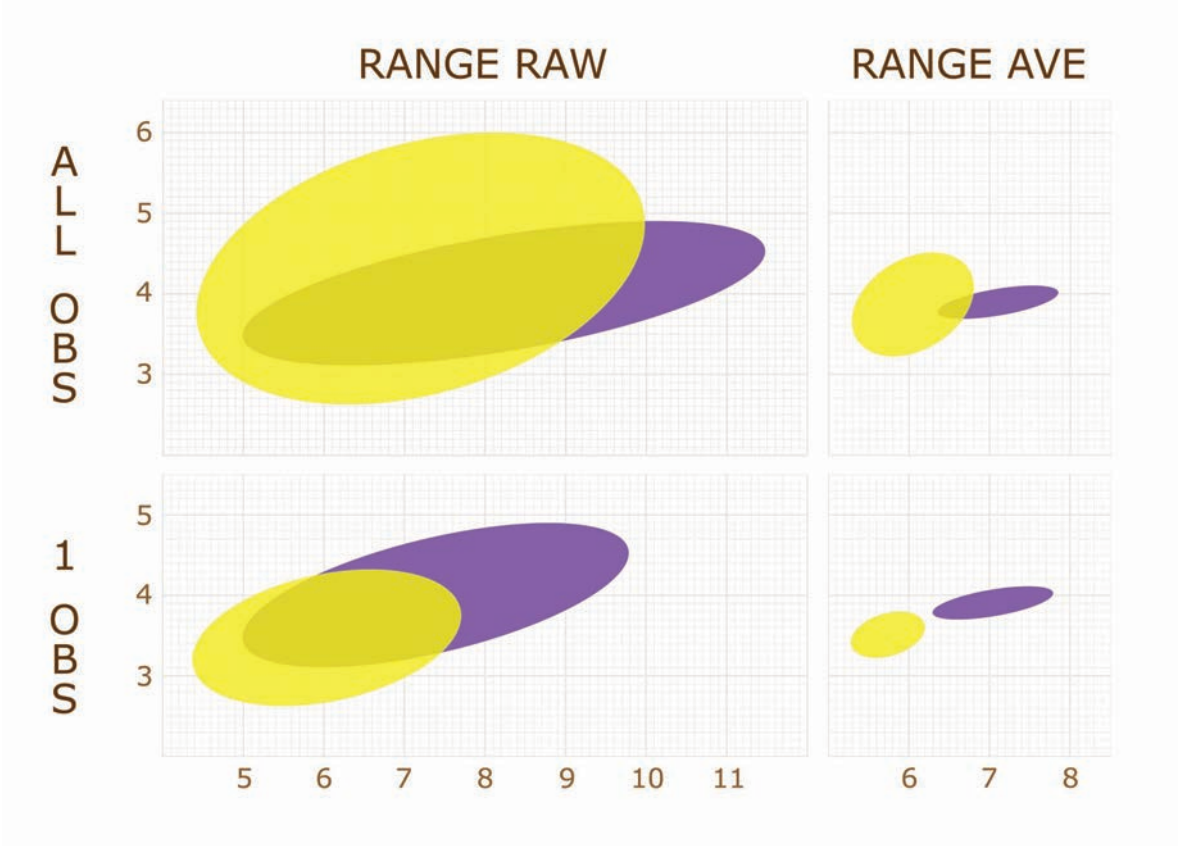

Figure 4: Comparison of spore size (µm) of *Pso. compressipes* (yellow oval) and *Pso. anticostica* (lilac oval) at the conclusion of our initial study. Length on x-axis and width on y. All measurements our own, using sequence-confirmed collections only. LEFT: range of raw data for all spores. RIGHT: range of average sizes for each specimen (min 20 spores/specimen). UPPER: data from all observers. LOWER: data for single observer (IS). Note that using average measurements reduces variation markedly, bringing out differences between species, and single observer measurements eliminate interobserver error due to individual differences of measuring. The combination separates the two species completely. While greater numbers of samples can be expected to cause some overlap, the effect will still be observed.

with a similar distribution. Most of the time they can be differentiated by spore size, despite significant overlap (Fig. 4); using average spore size will separate them better, and single observer measurement will refine the difference even more, as we reported in our article. Renée Lebeuf, who collected the holotype (Fig. 5) from Anticosti Island, also noted that *Pso. anticostica* seems more red in colour and occasionally *Pso. compressipes* seems to have a fuzzy cap, caused by upward projections of the long cells of the cap skin (Fig. 6). However, we have seen so few specimens, that for the moment we are not able to conclude whether these observations can be generalized to their species, or whether these characters may not also be seen in other species.

To underline how little we know about these species and how difficult it is to tell them apart, we describe two events after the report in Botany was accepted for publication.

Spore measurements and colour

Renée had some of her mushroom collections sequenced and among them one (see illustration with description of *Pso. compressipes*) was reported back as *Pseudoomphalina* cf. *kalchbrenneri* (i.e. if not the same, at least close). Having just worked on this group, we suspected this must be one of our eastern North American species. The spores were longer than any of our *Pso. compressipes* spores, and two average measurements fell outside the range for that species, but both measurements fit with *Pso. anticostica* (Fig. 7), suggesting it should be that species. Even the colour, although light, had some pink tones, which also fit with red tones noted for *Pso. anticostica*. However molecular studies placed the collection firmly in the *Pso. compressipes* clade (Fig. 2, pink background). Thus, this one collection has increased the range in spore size for *Pso. compressipes* from our report, thereby making it even more difficult to separate them by spore size (Fig. 7).

Figure 5: Holotype collection of *Pso. anticostica*, collected by Renée Lebeuf on Anticosti Island (HRL2133; DAOM970939). The florid crenulation-to-lobulation of the cap may be due to overmaturity, not a character of the species. We need more observation to learn reliable identification characters of this species. Photo: Jacques Landry.

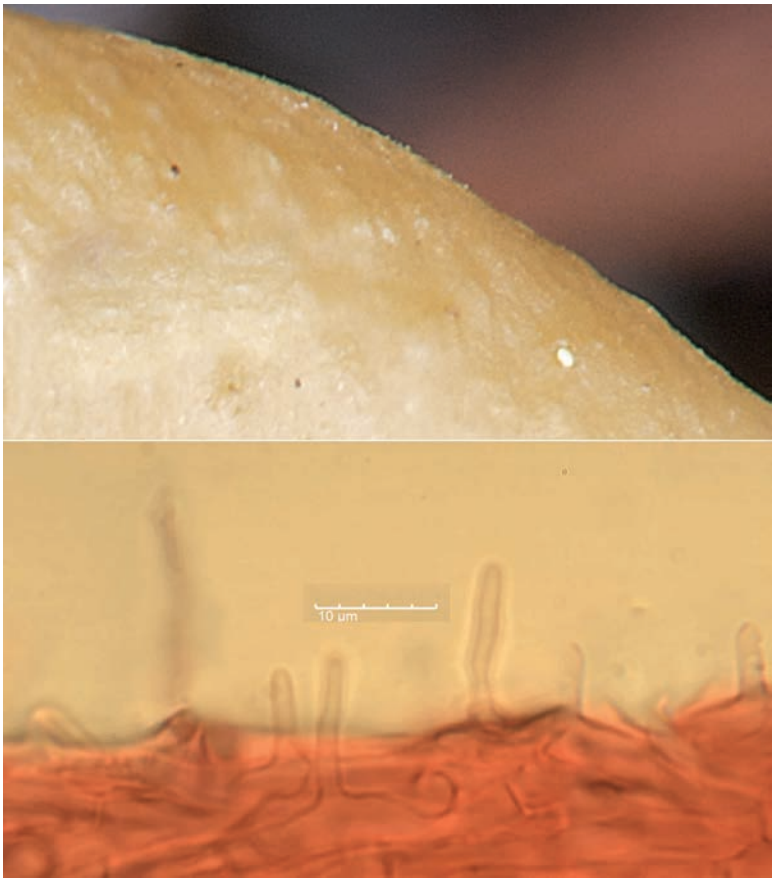

Figure 6: UPPER: cap of the Deer Lake *Pso. compressipes,* showing areas of fuzziness. LOWER: microscopic digitate hyphal projections identified by Renée, likely corresponding to the fuzzy areas of the cap. These were not seen on all specimens, so that we need more observations to know whether this is a useful identification character or something seen with other species as well.

Distribution

Irja came across a soil sample from Estonia that matched *Pso. compressipes*. Soil samples are bulk analyses of samplings of a portion of soil for the DNA of any or all species in the sample. Thus, it does not show the fruiting body, but merely indicates whether a species is present in the sampled soil of any specific place. Because the DNA of *Pso. compressipes* was found in Estonian soil, it means that the species must exist there, even if never reported or recognized.

First, this finding extends the range of what we thought as a North American species to northern Europe. That raises the question of why the species, clearly present in the soil, has never been recognized. The easy answer is that species of the complex are so alike, that one has been mistaken for the other. However, to date no collections with spore sizes as short as those of *Pso. compressipes* have been recorded in Estonia, or elsewhere in Europe. The epithet *compressipes* has been applied to some European specimens in the past, but these are now considered misapplications of the name, and the collections are considered conspecific with *Pso. kalchbrenneri*. In Europe only one other member of the complex has been described, *Pso. graveolens*. The macroscopic description of this species fits with any member of the complex, and the spore measurements fit best with *Pso. kalchbrenneri*, so these two species have been synonymized.

So long as there was only a single European species in the complex, this seemed logical, but now we know two things not known before: i) *Pso. compressipes* is also known to exist in Estonia, not far from the type region of Denmark, and ii) the spore measurements of *Pso. compressipes* may on occasion overlap those of *Pso. kalchbrenneri* considerably more than reported before. Therefore, at least theoretically, *Pso. graveolens* could be conspecific with *Pso. compresipes*. Unfortunately, this cannot be examined further, because the holotype for *Pso. graveolens* cannot be found. From a practical point of view, this is irrelevant, because *Pso. graveolens* was described after *Pso. compressipes*, so that in the case of conspecificity, the former name would become a later synonym. The foregoing was one of those Byzanthine discussions you may have to read several times, before you get the meaning, and then discover that it really does not matter... The long and short of it is that under the circumstances there seems no need to involve *Pso. graveolens*, but keep an eye out for *Pso. compressipes* in Europe.

Summary

This is the story of how a person who did not know the genus *Pseudoomphalina* existed, and who has in his life seen only one single mushroom of one species of the genus, got to be a world expert on this complex by virtue of following the advice of reviewers. As it turned out, the number of collections we needed to sequence after our first effort, in order to find the additional two species in North America, was seven. That is all it took to go from regional authorities to world experts! But as we see, after the report the new "world experts" still did not know these species very well. And the lead expert lost a Toonie bet to Renée in the process.

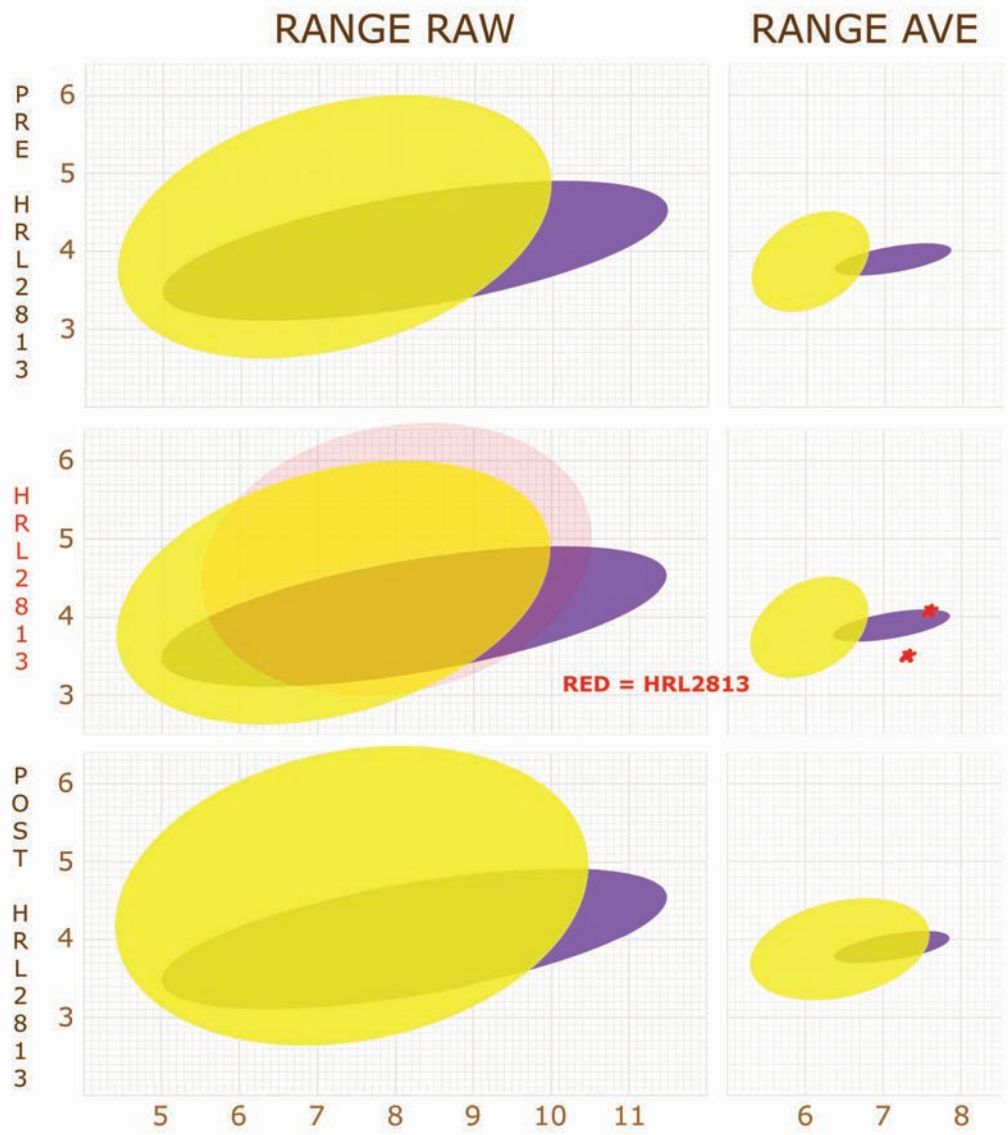

Figure 7: Revision of spore measurements because of a Renée's single collection, found after our initial report in Botany.
UPPER: The range and average spore size of *Pso. compressipes* (yellow oval) and *Pso. anticostica* (lilac oval), as reported in Fig. 4.
MIDDLE: The same graphic with Renée's later collection superimposed separately in red. The range size increase does not seem unusual, but the average size, which usually eliminates "noise" and becomes much more accurate and focussed, is significantly outside the range for *Pso. compressipes*. This is a very unusual finding.
BOTTOM: The spore size data revised from our previous publication after the addition of data from Renée's collection. The difference between the two species has now become very small, although spores of *Pso. anticostica* remain narrower than those of *Pso. compressipes*.

So, now you know that our *Pso. compressipes* has a wide range in spore size, and distribution to Europe according to soil sampling. **You read it here first!**

A brief description of *Pso. anticostica*, *Pso. compressipes* and *Psl. Pachyphylla* follows; the last two are confirmed from the province and the first likely also grows here.

Acknowledgments

In addition to the list in the peer-reviewed publication[1] of all the good folk who helped this happen, we thank Roger Smith and FNL, and Jacques Landry for the use of their respective photos. We thank Christian Lange at the Danish State Museum for pursuing the type of *Pso. graveolens* for us, and Pablo Alvarado for sequencing and permitting us to use the sequence of the last collection of *Pso. compressipes* from Quebec. And, here, to our embarrassment, we also need to add our gratitude for the loan of the Groves specimen from our own National Herbarium, DAOM, in Ottawa. Humble apologies for somehow omitting it and its staff from the acknowledgments in the Botany article. So sorry, Jen.

References

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Pseudoomphalina anticostica Lebeuf, Kennedy & I. Saar

MACROSCOPIC: Cap 1.5–4.5 cm, convex at first, depressed in the centre, becoming infundibuliform with age, with a margin incurved becoming strongly crenulate-lobate in old age; surface glabrous, hygrophanous, shiny; colour brownish orange to greyish orange. Gills adnate then decurrent, distant, becoming strongly forked and intervenose with age, thick, waxy, moderately broad; colour off-white becoming pale brownish orange in old age. Stem 2.8–5.0 × 0.4–1.6 cm, central, first cylindrical becoming flattened and flexuous with age, hollow; surface glabrous, concolorous with the cap, covered by white tomentum at base and bearing white rhizomorphs. Context thin; colour whitish. Smell farinaceous; taste farinaceous, bitter.

MICROSCOPIC: Spores 5.0–11.5 × 3.1–4.9 µm, ave. 7.2 × 4.0 µm, Q = 1.8, smooth, ellipsoid, amyloid. Basidia 29–50 × 6–7 µm, four-spored. Cheilocystidia 20–50 µm high, protruding up to 25 µm above the hymenium, 3–5 µm wide, 2–5 µm at the apex, abundant, filamentous, sometimes knobby, rarely branched, rarely capitate. Pleurocystidia rare, present close to gill edge, similar to cheilocystidia. Pileipellis (Fig. 3D) a cutis made up of repent hyphae 4–9 µm wide, mostly smooth, rarely finely incrusted. Clamps abundant in all tissues.

ECOLOGY, HABITAT & DISTRIBUTION: Putative saprobe. So far known from three collections, one made in mid-September in *Picea* needle litter in Quebec, Canada, and two made in early October on soil under young conifers in northern Minnesota, USA. For the time being, not documented in NL, but we suspect it may also be found here and has not been found because these species are rarely encountered here, and for this reason describe it, just in case you should meet it.

COMMENT: Given the small number of collections available, the sympatric *Pso. compressipes* and *Pso. anticostica* are difficult to distinguish macroscopically, but spore measurement may help, despite significant overlap. The colour of the fruitbodies might also be a distinguishing character, orange-brown in *Pso. anticostica* and tan to light-straw in *Pso. compressipes*. The specimens on Fig. 5 show marked crenulation of the cap edge, with larger specimens approaching lobulation; the two other collections look like the photo shown here, resembling the other species of the complex. We suspect that the size and florid crenulation-lobulation are the result of postmaturity hyperplasia, rather than distinguishing characters for the species. More collections will be necessary to confirm noted differences.

Pseudoomphalina compressipes (Peck) Singer

SYNONYMS: *Agaricus compressipes, Clitocybe compressipes, Clitocybula compressipes, Clitocybe farinacea, Pseudoomphalina farinacea, Clitocybe felleoides, Cantharellula felleoides, Pseudoomphalina felleoides*

MACROSCOPIC: Cap 2–4 cm, arcing downwards from an umbonate centre, edges lifting up to become infundi-buliform with crenate margin in age; surface glabrous, at times fuzzy or variously patterned, hygrophanous, opaque, but may be mildly translucent at edge; tan to light straw colour. Gills decurrent, narrow, close to subdistant, forked and interveined; colour off-white to straw. Stem 2–6 × 0.2–0.9 cm, central, ± equal, occasionally flattened ± longitudinally sulcate, pithy to hollow; surface glabrous; concolorous with to darker than cap, covered by white tomentum at base and forming white rhizomorphs. Context thin; colour whitish straw. Smell farinaceous. Spore deposit white.

MICROSCOPIC: Spores 4.4–10.5 × 2.6–6.4 µm, ave. 6.4 × 3.9 µm, Q = 1.7; smooth, ellipsoid; weakly to moderately amyloid. Basidia four-spored, 32–35 × 7–8 µm, clavate. Cheilocystidia 50–65 µm high, protruding up to 35 µm above the hymenium, 4–5 µm wide, 2–3 µm at the tips, uncommon to abundant, filamentous, thin-walled; pleurocystidia similar, rare to abundant, mostly present near gill edge. Pileipellis a cutis made up of repent hyphae 3–6 µm wide, mostly smooth, rarely finely incrusted; abundant cylindrical digitate projections 5–27 × 2–3 µm observed in one collection (Fig. 6). Clamps abundant in all tissues.

ECOLOGY, HABITAT & DISTRIBUTION: Putative saprobe. Terricolous on woody debris in open areas of leafy or mixed forests. Uncommon, occurs in scattered to moderate groups in the autumn; confirmed in northeastern North America as far west as Michigan. The only species in the complex documented in NL, it is now also known from Europe, found in a soil sample in Estonia.

COMMENT: Digitate projections of pileipellis hyphae have not been noted before in this group. We documented these projections in one basidiome of one collection (CMMF2076, Fig. 6). We did not find these structures on other collections or a different basidiome from the same collection. More observations are needed to know whether this is a differentiating character or an uncommon event in this and possibly other species of the complex. It differs from the sympatric *Pso. anticostica* by smaller spores.

Pseudolaccaria pachyphylla (Fr.) Vizzini & Contu

SYNONYMS: *Agaricus pachyphyllus, Clitocybe pachyphylla, Camarophyllus pachyphyllus, Omphalia pachyphylla, Pseudoomphalina pachyphylla*

MACROSCOPIC: Cap 1–3.5 cm, convex, usually with an umbilicate centre, becoming nearly plane; surface finely scaly, non-hygrophanous, tan to light straw colour. Gills sinuous, adnate, usually with small decurrent tooth, broad, thick, subdistant; colour light straw. Stem 2–5 × 0.15–0.25 cm, ± equal with slightly swollen base; surface glabrous to finely tomentose; pithy; concolorous with cap or slightly darker; white tomentum at base. Context firm; colour whitish. Smell farinaceous to near-rancid. Spore deposit white.

MICROSCOPIC: Spores 6.0–8.5 × 4.5–5.5 µm, ave. 7.1 × 4.9, Q = 1.4; smooth, weakly amyloid. Basidia four-spored. Cystidia none. Clamps in all tissues.

ECOLOGY, HABITAT & DISTRIBUTION: Putative saprobe. Terricolous in sandy, poor soil and moss of open areas in or near mixed forests, autumn, in scattered to moderate groups; uncommon; recorded in a boreal band across the Northern Hemisphere. Documented once in 16 years in NL.

COMMENT: Among differences from species in the *Pso. kalchbrenneri* complex are its smaller size, finely granular cap, non-decurrent to subdecurrent gills, larger spores, complete lack of cystidia, preference for poor, sandy soil, and circumpolar distribution. The ability to thrive in poor soil with little evident source of nutrition suggests that it may be worthwhile to question the lifestyle of this putative saprobe. Photo: Roger Smith.